Palaeodemographic studies at the hominin-bearing palaeocave site of Drimolen, South Africa

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Abstract

The primary goal of this thesis was to conduct a palaeodemographic analysis of the *Paranthropus robustus* and early *Homo* populations from the ~ 1.95 palaeocave site of Drimolen, South Africa. Palaeodemographic studies play an important role in the interpretation of extinct hominin species. All demographic studies are based on the concept of life-histories. Inspection of life-history characteristics provides information about the chronology and synchrony of growth, maturation, and aging milestones (i.e. age at weaning, age at first reproduction, interbirth interval, etc.). The manner and rate in which these systems change through time can provide insight into the evolution of the human lineage. Similarly, examining these landmarks can help broaden our understanding of the behaviour of extinct taxa. Through a combination of histological methods and extant ape and human analogues, hominin odontogeny is being utilised increasingly for the interpretation of hominin life-history characteristics. A Minimum Number of Individuals was established for the Drimolen material as well as primary identification and descriptions of unpublished dental material. For the purposes of clarifying species-specific odontogenetic patterns, dental formation and eruption patterns were identified. Additionally, a novel methodology for quantifiably assessing dental wear is proposed. Finally, a palaeodemographic interpretation of both the *P. robustus* and early *Homo* populations within the Drimolen assemblage was established and used to hypothesis as to the accumulation processes of the material. The demographic profiles of the Drimolen hominins were assessed against *P. robustus* from Swartkrans Member 1, a natural attrition profile of wild chimpanzee, a predation profile of wild chacma baboons, and the Drimolen fossil baboon population. It was found that the Drimolen *P. robustus* demographic profile most closely resembled that of the Swartkrans Member 1 *P. robustus* population, and the Drimolen early *Homo* demographic profile most closely resembled that of the wild chimpanzee.

1. Introduction

Through decades of palaeoanthropological study, a multitude of sites and species have been discovered. Increasingly, South Africa, and specifically ~2 Ma in South Africa, has become a focus for palaeoanthropological research. As discussed throughout this chapter, the dynamic nature of the fossil record in South Africa during this time period allows for research into areas such as environmental and dietary shifts, resultant changes in functional morphology, the advent of diverse tool technologies, etc.

This thesis will examine palaeodemography. As hominin-bearing sites in South Africa are primarily cave deposits, stratigraphy can be interpreted and accurate dates can be determined. The palaeo-cave site of Drimolen (Keyser et al. 2000), for example, provides a hominin assemblage that can be reasonably assumed to be unbiased, or at least minimally biased, by time averaging due to a relatively rapid deposition (Mallett 2015, Herries et al. in prep). Dating to ~1.95 Ma, the Drimolen hominin assemblage provides the opportunity to conduct a palaeodemographic study, interpret the life-histories of the species present, and examine the effects of changing environment and adaptive strategies on these patterns.

1.1 Demography

Demography is defined as the statistical study of populations. Demographic studies are widely used across a number of fields, including both zoology and anthropology. These studies are used to determine information such as population size, mortality rates, and sex ratios. This information allows researchers to interpret the behavioural patterns and biology of their subjects. Demographic studies have increasingly been applied to fossil collections in an attempt to broaden our understanding of early hominins in some of these areas including population density, landscape use, social structure, and behaviour. The size and fragmentary nature of these assemblages, however, (many of which are represented by isolated dental elements alone), limits the practicability and utility of these studies. Although the preservation bias leading to an overrepresentation of dentition has its drawbacks, a significant amount of information can nonetheless be gathered through

the inspection of dental remains. As Dean et al. (2001, pp. 628) expressed, "brain size, age at first reproduction, lifespan and other life-history traits correlate tightly with dental development". It is within the paradigm of assemblages biased towards dental elements that researchers have attempted to apply demographic methods for the purpose of understanding populations of early human ancestors.

That said, the use of extinct species as populations in demographic studies will produce erroneous results. That is, specific patterns regarding development or behaviour cannot be assumed to be constant across hundreds of thousands or even millions of years. Often, even individuals recovered from a solitary site may exhibit the effects of time averaging. When applying demographic methodologies to a fossil assemblage, this must be taken into account. Extinct populations that, due to depositional context, have been determined unlikely to exhibit time averaging will be referred to as *palaeo-populations* throughout this thesis. Unlike the definition of a true biological population which requires all individuals to belong to the same breeding group, a palaeo-population is defined here as consisting of individuals belonging to the same species which existed under equivalent adaptive pressures.

All demographic studies are based on the concept of life-histories. Inspection of life-histories provides information about the chronology and synchrony of growth, maturation, and aging milestones (i.e. age at weaning, age at first reproduction, etc.). The manner and rate in which natural selection influences the evolution of these systems' changes through time, can provide insight into the evolution of the human lineage specifically. Similarly, examining life-history landmarks can help broaden our understanding of the behaviour and biology of extinct taxa.

Many previous palaeodemographic studies have consisted solely of qualitative and subjective methodologies as evidenced by the subsequent demographic studies modelled after the methodologies of Mann (1975). These techniques cause problems for future researchers in regards to replicability, comparison to other studies, and interpretation in instances where methodology and criteria were not clear. However, while quantitative

methodologies are preferable in general for their replicability and objectivity, the nature of the assemblages in question and the hypotheses being tested sometimes precludes the strict application of quantitative methods due to statistically insignificant sample sizes, and the absence of non-qualitative metrics. In these cases, it is necessary to apply qualitative methods which, while encumbered by the aforementioned limitations, allow for otherwise unanswerable questions to be formatively addressed. While it is not always appropriate to avoid qualitative analysis, past studies have overemphasised these methodologies to a point where the studies become impossible to interpret or use as comparatives to quantitative studies. For example, conclusions drawn in studies such as Mann (1975) are based solely on subjective observation and as a result cannot be replicated for comparative purposes. It is crucial, as is the case in this study, to employ qualitative methodologies only when necessary and adhere to clear, standardised, objective, quantitative methodologies whenever possible.

1.2 A Review of Palaeoanthropology

Originally in palaeoanthropology, human evolution was viewed through a primarily Eur-Asian lens. When first discovered in 1857 in Germany, *Homo neanderthalensis* became the first widely recognised fossil hominin species. The species was named in 1864 by King as morphologically distinct from modern *Homo sapiens*. Earlier discoveries (1829; 1848) were largely ignored and the designation of *H. neanderthalensis* was initially disputed (Trinkaus 2014). Subsequent discoveries in Java increased this species count to two with the addition of *Homo erectus* by Dubois (1892). This species was originally considered to be a member of the chimpanzee clade and assigned the genus *Anthropopithecus* (Dubois 1892), however, further study placed the Java specimens within the genus *Homo* (Dubois 1937). The transition to anatomically modern human became clouded as discoveries in Rhodesia (now Zimbabwe) were said to represent a species named *Homo rhodesiensis* (Woodard 1921). Interpretation of these specimens, inclusive of *H. neanderthalensis*, varied based on the researchers proclivity to 'lump' or 'split'. That is, 'lumpers' are willing to allow a greater amount of intraspecific variability and so considered these specimens to represent an archaic morph of *H. sapiens*, while

'splitters' place more significance on morphological differences and so accept a greater number of distinct hominin species.

In 1925, however, the focus of palaeoanthropology was drawn out of Europe and into South Africa. The discovery and naming of *Australopithecus africanus* from Taung, propounded that there was an earlier ancestor to the European species discovered previously (Dart 1925) Since this discovery, *Au. africanus* has been identified across South Africa at multiple sites such as Sterkfontein and the Makapansgat Limeworks. Certain specimens later recovered from Sterkfontein were originally assigned to a different genus and species, instead named *Australopithecus transvalensis* (Broom 1936) and later changed to *Plesianthropus transvalensis* (Broom 1938; 1949). These specimens, such as the well-known Mrs. Ples (Sts 5), were defined as distinct from *Au. africanus* due to subtle morphological differences but are now considered to belong to the previously named species.

The presence of a 'robust clade' of australopiths at these South African sites, such as the type site Kromdraai B, led to the naming of a new genus and species: *Paranthropus robustus* (Broom 1938). Debate as to the phylogeny of these specimens is an issue still in continuance, resulting in the names *Paranthropus robustus* and *Australopithecus robustus* being used by researchers of differing views.

Certain specimens from Swartkrans, a site previously documented to have produced specimens attributed to *Paranthropus (Australopithecus) robustus*, were determined to be morphologically distinct from the australopiths present at the site. Instead, these specimens were attributed to the genus and species *Telanthropus capensis* (Broom & Robinson 1949). It was later proposed that these specimens belonged in the genus *Homo* however, due to the rules of nomenclature, they could not be attributed to *Homo capensis* and instead are currently referred to as South African early *Homo*.

The issue of 'robust' versus 'gracile' *Australopithecus* morphs and the presence of *Homo* in South Africa was further complicated by discoveries in eastern Africa. Excavations at

Olduvai Gorge produced specimens attributed to a new species: *Zinjanthropus boisei* (Leakey 1959). This species was later classified with the South African 'robust' australopiths and renamed *P. boisei*. Additional specimens from the Olduvai Gorge were attributed to the new species *Homo habilis* (Leakey et al. 1964). It was proposed that *H. habilis* was the progenitor species to *H. erectus*, which then gave rise to *H. sapiens* (Leakey et al. 1964).

Further discoveries in Ethiopia resulted in the naming of *Paraustralopithecus aethiopicus* (Arambourg & Coppens 1968), now referred to as either *Australopithecus aethiopicus* or *Paranthropus aethiopicus* (Olson 1985) and considered by some to represent either the species ancestral to *P. (Au.) boisei* or a temporally early morph of the same. A second progenitor species, *Australopithecus afarensis*, also discovered in Ethiopia, was proposed for *Au. africanus* and the australopiths as a whole (Johanson et al. 1978). The proposition of a shared progenitor species common to both *P. (Au.) robustus* and *P. (Au.) boisei* is problematic both because of the temporal and geographic disparity between the two species as well as the controversy surrounding the phylogeny of the former. The proposition of a progenitor species of the australopith clade is problematic in that the species suggested to rise from *Au. afarensis* is sampled prodominately from South Africa while the third proposed species in this lineage (*H. habilis*) is sampled from eastern Africa. This, of course, pushes specimens attributed to South African early *Homo* into further obscurity. Additionally, the suggestion that the previously established *H. erectus* exhibits great enough variability to be divided into an earlier African morph, *Homo ergaster* (Groves & Mazak 1975), and a later Asian morph, *Homo erectus*, convoluted the phylogeny of these species further.

1.2.1 South African Site Overview
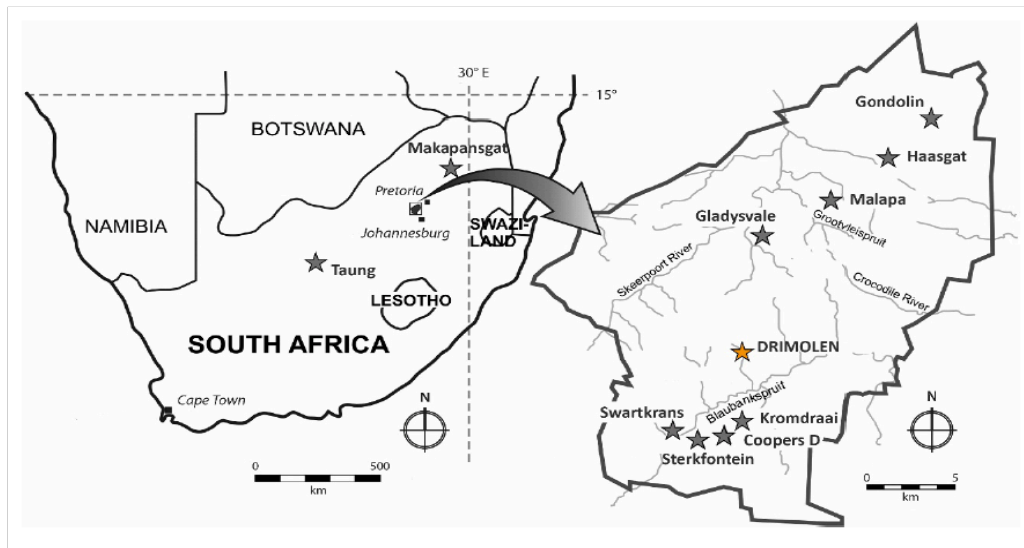
Figure 1: Map of South Africa with the 'Fossil Hominid Sites of South Africa' UNESCO World Heritage Area inset; Adapted from Pickering et al. 2011c

Between Johannesburg and Pretoria in the Gauteng Province of South Africa there is a roughly 400 km^2 area of dolomite that contains numerous caves that have yielded fossil hominins (Figure 1). Theses sites range from the first occurrence between 3.7 and 2.2 Ma (Sterkfontein Member 2) and the last occurrence sometime between 1.4 and 0.8 Ma (Swartkrans, Member 3 and Sterkfontein Member 5; Herries et al. 2009; 2010; 2013; Herries and Adams 2013; Stratford et al. 2014 see Table 1). However, the presence of hominin remains older than 2.58 Ma is highly debated (Herries et al. 2013) and hominin fossils in Member 3 at Swartkrans could represent reworking from older deposits (Herries and Adams 2013). This area is now designated as the 'Fossil Hominid Sites of South Africa' UNESCO World Heritage Site and is locally known as the Cradle of Humankind (Cradle; Figure 1). Apart from the Taung Type site at the Buxton-Norlim Limeworks (recording a single *Australopithecus africanus* cranium; the Taung Child at ~3.03-2.58 Ma; Herries et al. 2013), ~350 km to the south-west and the Makapansgat Limeworks, ~250 Km to the north-east (recording approximately 40 specimens of *Au. africanus*; 3.03-2.58 Ma; Herries et al. 2013), it is the only area in South Africa to have yielded hominin fossils older than ~1.1 Ma. Within the Cradle itself only four deposits are documented to have recorded *Australopithecus*. These are represented by Sterkfontein Members 2, 4 and

the Jacovec Cavern dated to between 3.67 and 2.01 Ma, *Au. sediba* from Malapa at ~1.98 Ma, and dental remains from ex-situ breccia at Gladysvale. All the *Australopithecus* fossils are older than 1.98 Ma. At about this time *Australopithecus* appears to go extinct and *P.* and early *Homo* first occur on the landscape. This is documented at Drimolen within the Main Quarry ~1.95 Ma and in Swartkrans Member 1 Hanging Remanent between 2.3 and 1.8 Ma, but likely between 1.96 and 1.80 Ma (Herries and Adams, 2013; Table 1). These two species persist on the landscape until sometime between 1.4 Ma and 0.6 Ma based on their occurrence at Coopers D, Swartkrans Member 3, and Sterkfontein Member 5 (see Table 1). However, the last definitive occurrence of *Paranthropus* is from Cooper's D in deposits slightly younger than 1.4 Ma (de Ruiter et al. 2009; Table 1) as its occurrence in the Swartkrans Member 3 deposits sometime between 1.3 and 0.6 Ma could be due to reworking from older deposits, as is well documented in some sites in the Cradle (Reynolds et al. 2007; Herries and Adams 2013).

Site	Member/Unit	Species Present	Date	Reference
Sterkfontein	Member 2	*Au. prometheus*	4.3 Ma, 3.7 or 2.6-2.2Ma	Stratford et al. 2014; Pickering and Kramers 2010; Herries and Shaw 2011; Clarke 2013; Partridge et al. 2003
Makapansgat Limeworks	Member 3	*Au. africanus/ Au. prometheus*	3.03-2.58 Ma	Herries et al. 2013
Buxton-Norlim Limeworks	Taung Child Type Site (Dart Deposits)	*Au. africanus*	3.03-2.58 Ma	Herries et al. 2013
Sterkfontein	Member 4	*Au. africanus/ Au. prometheus*	2.58-2.01 Ma	Pickering and Kramers 2010; Herries and Shaw 2011; Clarke 2013; Herries et al. 2010
Gladysvale	Breccia dumps	*Australopithecus*	<2.4 Ma based on internal sediment ages	Herries et al. 2013
Swartkrans	Member 1 Hanging Remnant	*P. robustus/* early *Homo*	Between 2.3 and 1.8 Ma; likely 1.96-1.80 Ma	Pickering et al. 2011b; Herries and Adams 2013
Swartkrans	Member 1 Lower Bank	Disputed	Between 2.3 and 1.7 Ma	Pickering et al. 2011b;
Malapa	Facies C-E	*Au. sediba*	~1.98 Ma	Pickering et al. 2011a
Drimolen	Main Quarry	*P. robustus/* early *Homo*	~1.95 Ma	Herries et al. *in prep*; Mallett 2015
Gondolin	GDA	*Paranthropus*	~1.8 Ma	Herries et al. 2006; Adams et al. 2007; Herries and Adams 2013
Kromdraai B	Member 3	*P. robustus/* early *Homo*	1.8-1.65 Ma	Thackeray et al. 2002; Herries et al. 2009; Braga & Thackeray 2003
Sterkfontein	Stw53 deposit (formerly Member 5A)	early *Homo*	1.8-1.6 Ma	Herries et al. 2009; Herries and Shaw 2011; Clarke 1985; Curnoe & Tobias 2006
Swartkrans	Member 2	*P. robustus*	~1.7-1.1 Ma	Herries et al. 2009
Coopers D	All	*P. robustus*	1.6-<1.4 Ma	de Ruiter et al. 2009
Sterkfontein	Member 5B (Oldowan Infill)	*Paranthropus/ early Homo*	1.4-1.1 Ma	Herries et al. 2009; Herries and Shaw 2011
Sterkfontein	Member 5C (Acheulian Infill)	early *Homo*	1.4-0.8 Ma	Herries et al. 2009; Herries and Shaw 2011
Swartkrans	Member 3	*P. robustus*	1.3-0.6 Ma	Herries and Adams 2013
Rising Star	Dinaledi Chamber	*Homo naledi*	Unknown	Berger et al. 2015

Table 1: Composite table of South African hominin-bearing sites found within the Malmani dolomite

A multitude of species including *Australopithecus africanus* (Dart 1925)*, Australopithecus sediba* (Berger at al. 2010)*, P. (Australopithecus) robustus* (Broom 1938)*,* and *Homo* sp. (Clarke 1985; Grine et al. 1996; Kimbel et al. 1997; Curnoe 1999; Grine 2001; Curnoe & Tobias 2006; Curnoe 2010) have been identified as well as other, more contentious species (e.g. *Australopithecus prometheus*; Dart 1948; Clarke 2006; 2013). Circa 2 Ma is a critical time period in South African hominin evolution. During this time period, the last occurrence of *Australopithecus*, the first occurrence of *P.,* and the first occurrence of *Homo* are all attested to by the fossil record (Herries et al. 2010) making the relationships of specimens within and between South African sites both complex and significant. As the South African Early Pleistocene (2.6-1.4 Ma) is characterized by high species diversity and change, it becomes crucial to examine this temporal context, particularly in areas reflective of highly adaptive variables such as diet, ontogeny, and mortality rates.

Sterkfontein (Figure 1) is perhaps the most complex of the South African hominin-bearing sites. The site is located within the Fossil Hominid Sites of South Africa UNESCO World Heritage Area, within the Sterkfontein Valley and is divided into a complex and disputed member system. Sterkfontein Member 4, dated to 2.58-2.01 Ma, has yielded primarily *Australopithecus africanus* (Broom 1947; Pickering & Kramers 2010; Herries et al. 2010; 2013; Herries & Shaw 2011). The last occurrence of *Australopithecus africanus* is currently the Sts 5 cranium from Sterkfontein Member 4 sometime around 2.07-2.01 Ma (Broom 1947; Pickering and Kramers 2010; Herries et al. 2010; 2013). It has been suggested, however, that there is a second species represented at Sterkfontein Member 4, named *Australopithecus prometheus* following a taxonomic attribution originally given to specimens recovered from the Makapansgat Member 3 in 1947 (Figure 1; Broom 1987; 1948; Kuman & Clarke 2000; Clarke 2013). Still others have argued for the presence of *P. (Australopithecus) robustus* at Sterkfontein based on a more 'robust' morphological suite than that seen in *Au. africanus*. The Little Foot specimen (Stw 573), recovered from Sterkfontein Member 2, has been argued to belong to *Au. prometheus* and is dated to either ~3.67 Ma based on cosmogenic nuclide burial dating, or 2.6-2.2 Ma based on combined uranium-lead and palaeomagnetic dating

(Pickering and Kramers 2010; Herries and Shaw 2011). Also documented are the Jacovec Cavern *Australopithecus* fossils that have also been suggested to be between 4.3 and 3.5 Ma based on cosmogenic nuclide dating (Partridge et al. 2003). Though Reynolds and Kibii (2011) assert that the presence of Equus in this deposit support and age of <2.3 Ma.

The manner in which Sterkfontein Member 5 is divided, both itself and between Member 4, is a topic of debate. Sterkfontein Member 5C, dated to 1.3-0.8 Ma (Herries et al. 2009), has yielded Acheulean stone technology and hominin specimens attributed to *Homo ergaster* and early *Homo* sp. (Tobias 2000). Sterkfontein Member 5B, dated to 1.4-1.1 Ma, has yielded Oldowan stone technology and hominin specimens attributed to *P. robustus* and *Homo* (alternatingly called *Homo ergaster, Homo erectus* and early *Homo* sp.; Tobias 2000). The oldest section of Sterkfontein Member 5A (Stiles & Partridge 1979) is the most heavily debated; more so because the significant specimen Stw 53 is derived from this region. Kuman & Clarke (2000) argue that the stratigraphic layer containing this specimen is part of Member 4 and so dates to ~2 Ma. Herries & Shaw (2011), however, suggests that Stw 53 instead derives from an infill layer between Members 4 and 5 and dates instead to 1.8-1.5 Ma.

Additional debate surrounds the taxonomic attribution of this specimen. If Stw 53 represents *Australopithecus* rather than early *Homo* (as suggested by Clarke 2008; 2013) then this specimen would represent the LAD for *Australopithecus* at 1.8-1.5 Ma (Herries and Shaw 2011). However, if Stw 53 is included instead within the genus *Homo*, the last appearance date (LAD) of the genus *Australopithecus* is 1.98 Ma based on the first and last appearance date of *Australopithecus sediba* at Malapa (Figure 1; Pickering et al. 2011a).

Swartkrans is also located within the Fossil Hominid Sites of South Africa UNESCO World Heritage Site in the Gauteng province, South Africa (Figure 1). Swartkrans is divided into five main depositional and geological units: Member 1 (Member 1 Lower Bank and Member 1 Hanging Remnant), Member 2, and Member 3, Member 4, and Member 5 (Brain, 1993). *P. robustus, Homo* sp., and stone and bone tools have been

recovered from Swartkrans Member 1, dating to sometime between 2.3 and 1.7 Ma, but likely after 2 Ma, (Pickering et al. 2011b; Herries and Adams 2013). Member 2 has yielded both early *Homo* and *P. robustus* specimens, dating to 1.7-1.5 Ma (Brain 1993; Watson 1993; Herries et al. 2009). Member 3 contains *P. robustus* and dates to sometime between 1.3-0.6 Ma, (Brain 1993; Watson 1993; Herries & Adams 2013; Granger et al. 2015). *P.* fossils have also been recovered from much younger Members where they are considered to be intrusive (de Ruiter 2003). Herries and Adams (2013) have also questioned whether the same maybe true of the Member 3 material. While *P. robustus* has been recovered from other members, it is the Swartkrans Member 1 *P. robustus* material included in this thesis as the relatively short depositional period and apparent lack of mixing is suitable for comparison with the Drimolen *P. robustus* material (discussed below).

Kromdraai (Figure 1) is divided into two sites: Kromdraai A and Kromdraai B. Kromdraai A yields non-hominin faunal material while Kromdraai B yields *P. robustus* material and one suggested early *Homo* specimen (Braga & Thackeray 2003). Kromdraai B Member 3 is suggested to date to 1.78-1.65 Ma (Thackeray et al. 2002; Herries et al. 2009). It is this member that all in-situ hominin material has been recovered, although Thackeray et al. (2002) has suggested the type specimen comes from the older, >1.95 Ma, Member 1 deposit based on associated breccia colour on the specimen.

Gondolin (Figure 1) dated to ~1.8 Ma, has yielded only two hominin specimens amongst a large non-hominin faunal collection (Menter et al. 1999; Adams & Conroy 2005; Herries et al. 2006; Adams et al. 2007; Adams 2010; Herries & Adams 2013). These specimens have been attributed to *P. robustus*. While alone these specimens reveal nothing about demographics and populations, the large absolute size of one of the specimens has lead to the examination of possible indicators of secondary maturation in *P. robustus* (Lockwood et al. 2007; Grine et al. 2012). Coopers A (Figure 1), dated to 1.6-<1.4 Ma, has also been reported to have yielded *P. robustus* however, this material has since been lost, while materials recovered from Coopers D (Figure 1) are few and poorly preserved (de Ruiter et al. 2009).

The South African fossil is complex and dynamic indicating high taxic diversity within such a geographically constrained region as well as evidence of relatively rapid morphological change and speciation. Due to this, the study of life-history and behavioural patterns that may help to identify differences, change trajectories, and the specific adaptive pressures each distinct species was under becomes crucial.

1.2.2 Drimolen

The Drimolen locality was discovered in 1992 by Andre Keyser and has since become one of the richest hominin-bearing sites in South Africa yielding both *P. (Australopithecus) robustus* and early *Homo* specimens (Keyser et al. 2000; Keyser 2000; Moggi-Cecchi et al. 2010). Drimolen is part of a dolomitic palaeocave system formed within the Monte Cristo Formation of the Malmani Dolomite (Keyser et al. 2000). Until recently, Drimolen was thought to consist of a series of related deposits that were considered to be temporally similar, sometime between 2.0 and 1.4 Ma based on biochronology (Keyser et al. 2000; Herries & Adams 2013). Over the last 5 years, detailed work at the locality has enabled the identification of two distinct palaeocave infills: the Drimolen Main Quarry (DMQ), which has yielded all the hominins remains and is dated to around 1.95 Ma; and the Drimolen Makondo (DMK), which is dated to ~2.6 Ma. While the stratigraphic relationship of these deposits remains undetermined as they occur 50m apart, they have shown to be distinct in terms of their age and the species present (Rovinsky et al. 2015; Herries et al. in review; Adams et al. 2016). The two infills are thus similar to other localities where more than one deposit occurs in close proximity, such as Kromdraai A and B. In a similar manner, Kromdraai B contains hominins while Kromdraai A does not and the infills consist of distinct faunal taxa. Similar situations occur at the site of Cooper's (A-D). To date the majority of excavation has occurred within the Main Quarry deposit and it is this area that will be the focus of this study. As is the case in nearly all fossil-bearing localities in this region, the Main Quarry was heavily disturbed by lime miners in the early 20th century (Keyser et al. 2000; Figures 2 & 4).
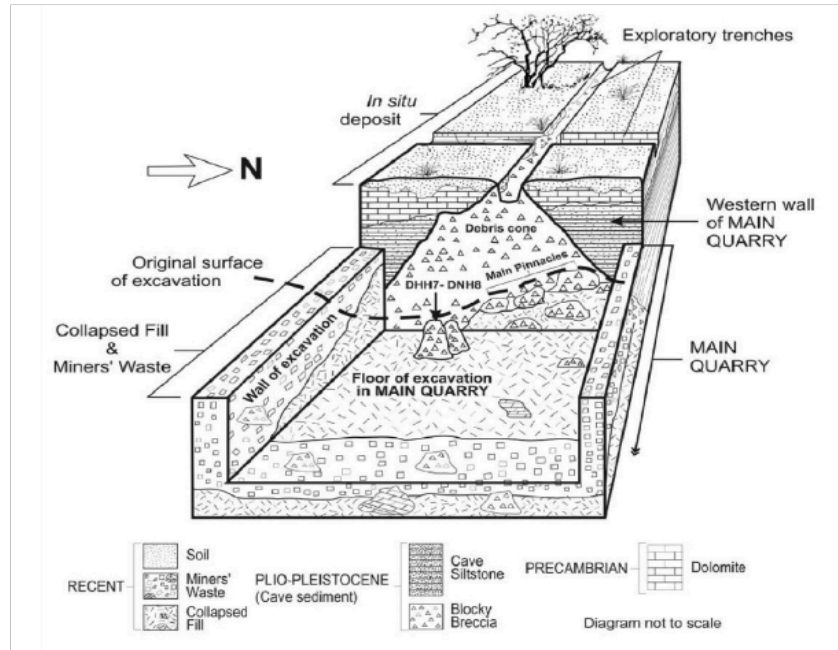
Figure 2: Drimolen Main Quarry stratigraphic diagram; From Keyser et al. (2000)

1.2.2.1 The Drimolen Main Quarry
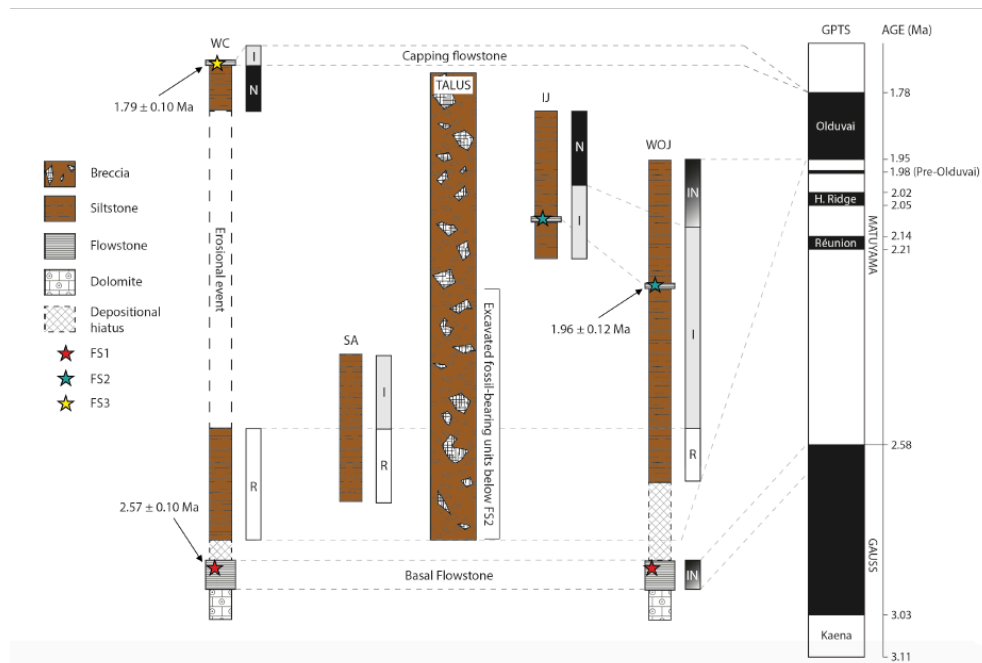
Figure 3: Drimolen Main Quarry magnetostratigraphy; From Mallet 2015

The DMQ appears consist of a single, large cavern with a vertical entrance. The oldest deposit in the DMQ is represented by a basal flowstone layer (FS1), formed along the base and parts of the walls of the former cavern (Figure 3). This thick speleothem layer has been dated by uranium lead (U-Pb) to 2.67 ± 0.10 Ma (2.77-2.57 Ma) and shows an intermediate normal to reversed magnetic polarity (Herries et al. in prep). It has been suggested that this deposition occurred at the end of the Gauss Chron, near the Gauss-Matuyama boundary at approximately 2.58 Ma (Herries et al. in prep). A temporal hiatus likely occurred between FS1 and the overlaying fossiliferous layer (FBU1) as is common in these sites (Pickering et al. 2011b). This is supported by the presence of *Equus* near the base of FBU1, which suggests an age of less than 2.33 Ma (Geraads et al. 2004). Nearly all hominin material originates from this layer. FBU1 consists of two phases of sedimentation. The primary phase comprises a talus cone formed from the input of surface sediments from an entrance in either the roof or upper walls of the cave chamber. The secondary phase consists of finer winnowed material, which has been reworked from the talus via water action during its infill history. A remnant talus cone is present on the western side of the DMQ excavation area. The western portion of the DMQ deposit is *in situ*, preserving a portion of a talus cone indicating a vertical entrance, while the central portion represents collapsed *ex situ* material, and the eastern portion likely represents miner's rubble (Figure 4; Herries et al. in prep). The sediments of FBU1 show a reversed polarity while the thin speleothem layer above it (FS2) shows an intermediate polarity (Herries et al. in prep). Deposits above FS2, FBU2, have intermediate to normal magnetic polarity showing the occurrence of a magnetic polarity reversal. FS2 has been U-Pb dated to 1.96 ± 0.12 Ma (2.08-1.74 Ma) and indicates that this reversal is the base of the Olduvai SubChron at approximately 1.95 Ma (Herries et al. in prep). After the deposition of FBU2 there is an erosional event, which is then capped by a third speleothem layer (FS3; Herries et al. in prep). FS3 has a normal polarity and is U-Pb dated to 1.79 ± 0.10 Ma (1.89-1.69 Ma), placing it within the later part of the Olduvai Chron (1.95-1.78 Ma; Herries et al. in prep). As such, all the hominin fossils occur within layers dated to between 2.3 and 1.8 Ma, almost identical to ages for the Member 1 Hanging Remnant at Swartkrans. However, the identification of a magnetic reversal in deposits equivalent to the hominin bearing breccia means that the majority, if not all the hominins were

deposited during a short time period around 1.95 Ma (Mallett 2015; Herries et al. in prep.). Thus it is an ideal situation for a palaeodemographic study, as will be discussed in subsequent chapters.
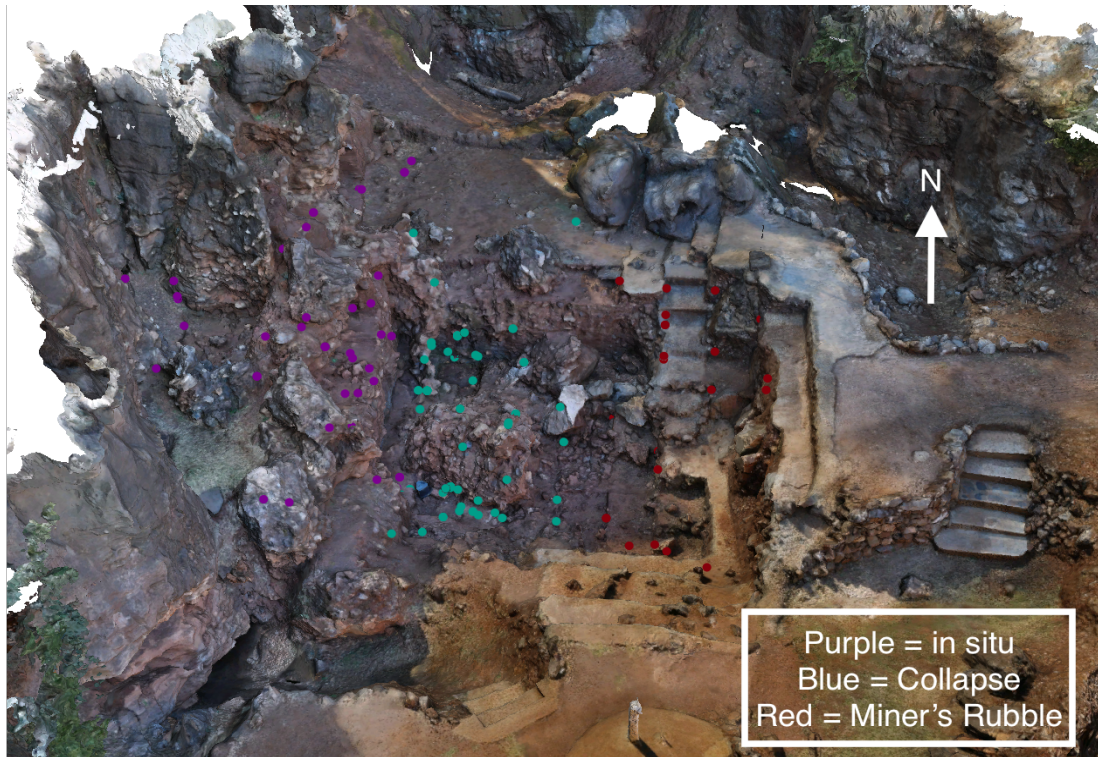
Figure 4: Drimolen Main Quarry hominin context

1.2.2.2 Assemblage Composition

Archaeology recovered from the Main Quarry is not expansive, represented by only seven stone tools and at least 22 fossilised bone fragments purported to represent bone tools similar to those found at Swartkrans (Keyser et al. 2000; Backwell & d'Errico 2008). The faunal sample is extensive with carnivores, bovids, non-human primates, and micromammals (O'Regan and Menter 2009; Nieuwoudt 2015; Adams et al. 2016). Both *P. robustus* and early *Homo* specimens are found within the hominin assemblage. The former is represented by 81 specimens and the latter by 15 specimens, with 37 indeterminate hominins. The assemblage consists primarily of dental elements with only 33 of 133 specimens representing postcranial material. The Drimolen *P. robustus* assemblage is distinct in multiple ways. Firstly, the most notable specimen from this

collection is DNH 7. This individual consists of a nearly complete cranium and mandible of a lightly built, female *P. robustus* (Keyser 2000). Not only is this specimen the most complete example of the species to date, but it also differs from the sample of young adult males preserved at Swartkrans (Keyser et al. 2000; Lockwood et al. 2007; Moggi-Cecchi et al. 2010) contributing to the understanding of individual variation, intra-specific variation, and sexual dimorphism within the species.

A preliminary study of DNH 7 and an associated male mandible (DNH 8) has been undertaken (Keyser 2000) as well as an analysis of a portion of the dental specimens (Moggi-Cecchi et al. 2010). However, a full morphological analysis of the hominin remains has not been conducted, leaving the assemblage without a minimum number of individuals (MNI) or age at death profile. Some research to this effect has been conducted (Tafforeau et al. 2011; Smith et al. 2015). These studies take the first steps towards creating a reliable and quantifiable methodology for age at death and palaeodemographic interpretations. However, as will be discussed in detail in following chapters, these studies are preliminary and demographic profiles conducted across sites within the Fossil Hominid Sites of South Africa UNESCO World Heritage Site have been determined using qualitative and subjective methodology (e.g. Mann 1975). The apparently rapid deposition of the Drimolen Main Quarry hominin material renders this assemblage ideal for palaeodemographic analysis.

1.3 Aims

The broad aims of this study are as follows:

1. Assess previous palaeodemographic methodologies
2. Determine the Number of Individual Specimens Present (NISP), Minimum Number of Individuals (MNI), and age at death profile for the Drimolen hominin assemblage
3. Assess odontogenetic patterns of *P. robustus* at Drimolen
4. Assess dental wear patterns of *P. robustus* at Drimolen
5. Determine the palaeodemographic profile of *P. robustus* at Drimolen

1.4 Significance of Research

Drimolen is the second richest *P. robustus* site after Swartkrans. Pursuance of the abovementioned aims will provide accurate age at death profiles for *P. robustus* and test existing paleodemographic hypotheses. This study will also lay the groundwork necessary to develop a pattern of dental eruption specific to *P. robustus*. These techniques developed as part of this research may then be applied to other extinct hominin species in addition to extinct and extant primate populations. Estimating the paleodemography of an early hominin palaeo-population as proposed by this study is crucial to understanding group dynamics and social patterns. When combined with both isotopic analysis of landscape pattern use and diet, and the archaeological evidence (Keyser et al. 2000; Backwell & d'Errico 2008), it will become possible to establish how *P. robustus* was using the South African landscape.

A comparison between the resulting Drimolen data set and that of the nearby and penecontemporaneous *P. robustus* yielding palaeocave site of Swartkrans would also be beneficial. The similar age and location of the two caves sites (approximately 7km; Keyser et al. 2000), combined with the markedly different age at death results for the two assemblages, raises further research questions relating to processes such as site formation and taphonomy. For the first time, this work will create a paleodemographic model for the Drimolen *P. robustus* assemblage. It will also help to build a methodological basis for undertaking similar analyses of *P. robustus* material from other sites, as well as for other hominins such as early *Homo* and *Australopithecus*.

1.5 Thesis Structure

Chapter 2 provides background into palaeodemography and life-history as well as methodologies historically applied to such questions for the purpose of elucidating the trajectory of this area of research. Chapter 3 assesses the validity of standard palaeodemographic analysis versus histological assessment. Chapter 4 discusses the Drimolen hominin assemblage as a whole and presents anatomical descriptions and species attributions of the unpublished hominin material. Additionally, this chapter presents an MNI and a relative age seriation of the Drimolen hominin material. Chapter 5

analyses data drawn from the relative age seriation and proposes an odontogenetic profile for *P. robustus* at Drimolen. Chapter 6 introduces a novel method for analysing dental wear of fossil individuals. Chapter 7 presents a palaeodemographic analysis of the hominin species present at Drimolen. Chapter 8 presents the conclusions of these studies and discusses future research and implications. Appendix 1 provides a dental anatomy reference. Appendix 2 provides the anatomical descriptions of the unpublished hominin dental material. Appendices 3-5 relate directly to specific studies discussed below.

2. Demographic Analysis

2.1 Life-History and Palaeodemography

Palaeodemographic studies play an important role in the interpretation of extinct hominin species. All demographic studies are based on the concept of life-histories (Robson & Wood 2008). The life history theory holds that behavioural and physiological traits can be understood and interpreted through study of life-history characteristics (Leigh 2001; Yampolsky 2003; Allaby 2010). These characteristics include growth, maturation, and aging milestones (i.e. age at weaning, age at independence from mother, age at first reproduction, interbirth interval, etc.; Leigh 2001; Kaplan et al. 2000; Robson & Wood 2008). The manner and rate in which these systems change through time can provide insight into the evolution of the human lineage. Similarly, examining these landmarks can help broaden our understanding of the behaviour of extinct taxa.

It has been hypothesised that particular life-history characteristics are linked to specific morphological features, which are, in turn, linked to certain behaviours. For example, it has been proposed that exceptional longevity and extended juvenile periods can be linked to large brains relative to body size (Kaplan et al. 2000). The presence of morphological features such as an encephalised brain are thought to correlate with behaviours such as male support of reproduction by provisioning females and young, and support of reproduction by post-reproductive individuals (the 'Grandmother Hypothesis'; Hawkes et al. 1989; Hawkes et al. 1997; Kaplan et al. 2000). These behavioural changes are thought to manifest concomitantly with encephalisation due to associated psychological attributes such as an increased capacity for learning, cognition, and insight (Kaplan et al. 2000). These changes are evident in life-history characteristics due to the need to adjust the rate and timing of growth, both to facilitate the development of a larger brain, and allow for an extended juvenile period (Smith 1989). The evolution of hypotheses such as these are discussed in detail below.

As demography examines the behaviours of populations, the synchronous relationship between anatomy, life-history, and behaviour becomes crucial to understanding these extinct species. Dentition, as discussed in Chapter 1, makes up the majority of the fossil

record. Developmental markers are preserved within dental microstructure, as enamel and dentine are deposited in a regular and predictable pattern and clearly display irregularities at key points in an individual's life (Bromage & Dean 1985). In the example given above, for instance, a delayed rate of permanent tooth eruption and a later occurring neonatal line (irregularity in enamel deposition at weaning age; Rushton 1933; Schour 1936), are two indicators of a prolonged juvenile period. It is for these reasons that the study of hominin dental remains, through the lens of life-history and demography, is crucial to the understanding of extinct human taxa.

In extant populations, once identified, the ages of the individuals comprising the group must be determined. This is a simple enough task when studying living populations and deceased populations of modern species that can be aged with confidence using dental development patterns specific to the species. Determining the sex of extant individuals is also a relatively simple task. When studying extinct taxa, however, determining the sex of the represented individuals is often difficult, as sexual dimorphism is not well understood in extinct hominin species. Determining age at death of fossil individuals is also difficult as well as multifaceted. External factors such as environmental pressures can also influence life-history and development, as exemplified in the 'wild effect' (per Zihlman et al. 2004).

Historically it was believed that the life-history of early hominins would align with either great ape life-history or modern human life-history. It is now known that not only can early hominin life-history not be defined by these binary categories, but the concept itself is false. A homogenous great ape development pattern does not exist as each species within this group exhibits unique life-histories. The same is likely true for early hominin species. While this is not to say broad primate-wide patterns do not apply, specific life-histories and ontogeny appears to be influenced more by adaptive strategy and behaviour than phylogenetic relatedness. Disparities in these patterns, then, can be assumed to be indicative of varying adaptive responses to varying pressures.

As these theories became more broadly accepted, research focus shifted towards histological methodologies. These studies take advantage of the internal microstructure of an individual's dentition to interpret specific developmental patterns. As enamel and dentine are deposited in a regular and predictable manner, and life-history landmarks such as weaning can be identified based on irregularities within these deposited striae, histological assessment of dentition can produce a developmental pattern specific to the individual in question.

2.2 Background to Palaeodemographic Studies

2.2.1 Life-History Determination and Commonly Utilized Techniques

As previously discussed in this chapter, the identification of life-history characteristics and overarching life-history patterns is essential to the understanding of a species' ontogenesis and behaviours as well as demographic interpretations. Life-history is the culmination of characteristics that detail an animal's life from conception to death (Ross 1989). Due to the interconnectedness of these variables, it is difficult to ascertain which is the dependent variable and which is the independent variable. For example, encephalisation has been clearly linked to an extended juvenile period (Kaplan et al. 2000; among others discussed further below) however, it is difficult to determine which is the causal factor. External variables such as diet and environmental pressures have also confounded the identification of these correlations in extant species and will be discussed in more detail below. These issues must be taken into account when determining life-history characteristics and drawing conclusions in regards to broad species- or genus-wide patterns.

Additionally, small sample sizes within the fossil record, poor understanding of diet and environmental pressures, and a changing understanding of these correlations have made life-history determination an extremely complex issue. Researchers are restricted to only what preserves to the present day. Examination of features such as body mass, which can be estimated based on axial osteological remains, brain mass, which can be calculated based on cranial remains, and dental development have been used to infer life-history patterns. The latter has been studied most intensively for a few key reasons. Firstly, as

discussed previously, dental remains comprise the majority of the fossil record while skeletal remains are relatively sparse due to preservation bias. Secondly, developmental markers are preserved in dentition at a microscopic level. Morphological features such as striae of Retzius (Appendix 1) and hypoplastic pits and lines are particularly useful in this regard. Striae of Retzius refer to small bands found within the microstructure of dentition. These bends represent the regular and predictable deposition of enamel during the formation of the tooth (Smith 2005). These striae, also referred to as incremental growth lines, allow researchers to determine the rate of dental development in specific elements and so infer dental development rates and patterns within individuals (Smith et al. 2015). Hypoplastic pits or lines indicate physical or emotional trauma that interferes with this regular development and can be correlated across dental elements within individuals to interpret life-history characteristics such as age at weaning (Schwartz et al. 2006; Smith 2013). Expanding this information to a species- or genus-wide pattern, however, remains problematic due to the small sample size hindering the determination of variability within larger groups.

2.2.1.1 Body Mass and Life-History

It is a generally accepted hypothesis that primate life-histories fall into one of two categories based on body mass: 'live-fast, die-young' or 'live-slow, die-old' (Ross 1998). The former refers to small-bodied primates which develop quickly, breed more rapidly, produce more offspring, and die younger, while the latter refers to large-bodied primates which develop and breed more slowly, produce fewer offspring, and live longer (Ross 1998). As a coarse grained calibration of life-history to body mass, this hypothesis holds true for extant primates, excluding modern humans (Ross 1998). The synchronous nature of the relationship between body mass and life-histories in extant primates raises the hypothesis that body mass could be used to predict longevity in extinct taxa, provided that the relationship remains consistent.

However, attempts to refine the coarse grained correlation between the morphological variables and life histories to produce a predictive model have proven to be problematic. For example, in a study designed to investigate the relationship between body mass and

primate life-history patterns, Ross (1998) concluded that brain mass rather than body mass was the principal correlative factor to longevity. In general terms, this hypothesised refined causal relationship between brain mass and longevity has been supported by subsequent studies (Kaplan et al. 2000; among others). The debate regarding whether longevity is best predicted by brain mass or body mass is arguably complicated by the fact that Ross (1998) found brain mass increased through linear scaling as body mass increased in extant primates. In other words, brain mass and body mass are causally related, and both of these morphological characteristics are in turn predictive of longevity. That is, brain and body mass correlate equally with the proposed life-history pattern hypothesis (Ross 1998), and as such it is actually the *ratio* between these two variables that is predictive of longevity. Despite the phylogenetic relatedness of extant primates and extinct hominin taxa, the demonstrated presence of uniquely encephalised brains in the latter calls into question the potential utility of applying and extant analogue to predict life history variables (Ross 1998). This is because the regression model that governs the relationship between brain mass and body mass ratios in extant primate taxa is violated by encephalised hominin taxa, including *Homo sapiens*. While the possibility of establishing a hominin specific regression model that reflects the relationship between brain mass and body mass ratios and longevity is hypothetically possible, the use of extant primate analogues is, for the reasons outlined, inappropriate. The development of a regression model based solely on the fossil record would not only be a highly circular approach but is also hindered by the extremely small sample of the postcranial remains necessary for body mass estimation.

2.2.1.2 Brain Mass and Life-History

As brain mass, rather than body mass, was suggested to be the true catalyst for broad changes in life-histories it was hypothesised that brain mass would correlate with more specific life-history characteristics such as gestation length, inter-birth intervals, maturation rates, etc. (Smith et al. 1994; Ross 1998; Kaplan et al. 2000; Godfrey et al. 2001; among others). This link was said to have arisen as a result of physiological mechanisms (i.e. foetal brain growth costs) and the adjustments required for the benefits of expanded cranial capacity to be realised (Smith 1989). However, many of the same

obstructions that exist in the use of body mass for life-history determination carry over to the use of brain mass.

2.2.1.3 Dental Development and Life-History

Body mass, brain mass, metabolic rate, and most reproductive variables (gestation length excluded) are relatively plastic and often modified substantially in response to environmental factors (Smith 1989). Maturation of hard tissues such as dentition and the skeleton, however, exhibit far less variation making areas such as odontogenesis ideal for tracking life-history landmarks (Smith 1989). Formation and eruption patterns appear more consistent than traits such as body or brain mass and so make for a better comparative model (Smith 1989). Due to the nature of the internal structure of dental elements discussed previously, odontogeny can be confidently interpreted and, in some cases, predicted (Bromage & Dean 1985).

As dentition is far less plastic than other potential life-history predictors, both life-history characteristics and anatomical traits correlating with odontogenesis needed to be identified. Gathering information from a number of different studies, Smith (1989) tested for a correlation between dental eruption and ten life-history and size variables. These included female body weight, birth weight, gestation length, age at weaning, interbirth interval, age at sexual maturity in females, lifespan, neonatal brain weight, and adult brain weight. This analysis showed a strong correlation between dental stages and these variables ($r = 0.98$ to $r = 0.99$), and brain weight and all other variables ($r = 0.83$ to $r = 0.95$; Smith 1989). Smith (1989) asserted that dental variables tend to correlate at least as well with reproductive variables as reproductive variables correlate with each other ($r = 0.92$ and $r = 0.89$, respectively). This study led Smith (1989) to conclude that brain size and dental maturation, in particular age at M1 eruption, are reliable markers for life-history studies. While the assertion that brain size is a reliable predictive characteristic has been questioned (Ross 1998; Macho 2001), dentition remains an important interpretive tool.

To further examine the question of life-history interpretation from odontogenesis, Smith et al. (1994) compiled all available data on extant primate dental eruption. This sample included 46 primate species representing modern human, great apes, and lesser primates (Smith et al. 1994). Preliminary analysis showed many primate species were born with dentition in occlusion and only modern humans and great apes remained toothless up to a month after birth (Smith et al. 1994). Through examining the life-histories of these species in relation to their relative dental eruption pattern, Smith et al. (1994) concluded the mean age of tooth eruption related directly to mean adult body mass and brain weight. These two factors are, of course, reflected in ontogenetic patterns and may be influenced by a different causal factor. As discussed previously, body and brain mass can present a false interpretation of life-history (Ross 1998). The characteristic separating modern humans and the great apes from other primates in delayed dental eruption may in fact be influenced by an extended juvenile period. This becomes problematic when applying these patterns to fossil species as the presence or absence of an extended juvenile period if deferent species is highly debated. Due to this, it would be preferable to avoid the necessity to rely on brain mass for life-history determination of fossil hominins.

It has been proposed that molar odontogenesis is more closely correlated with anatomical features and life-history characteristics than anterior teeth (Zuckerman 1928; Smith 1989). With the aim to solidify the relationship between molar formation timing and life-history, Macho (2001) examined all extant and extinct primate developmental data published at this time, paying attention to molar crown formation and specifically brain size and female body weight. The majority of results indicated a strong correlation between molar crown formation times and both female body mass and brain size as well as a consistent scaling relationship between body and brain size (Macho 2001).

Certain primate species, however, departed from the correlative relationship between brain/body mass and molar formation timing. Macho (2001) found some large-bodied primates, such as *Gorilla gorilla* and *Theropithecus oswaldi*, demonstrated significantly shorter molar crown formation times than predicted based on brain and body mass. The reverse situation, however, was not recorded in species, such as *Homo sapiens*, that

depart from the brain and body mass allometry due to an encephalised brain (Macho 2001). This suggests the deviation in *Gorilla gorilla* and *Theropithecus oswaldi* is due to brain size increase caused by a linear scaling of body to brain mass as opposed to non-linear encephalisation.

Macho (2001) theorised multiple possibilities for these departures as well as the implications for interpretations of early hominins. Examining the manner in which these evolutionary changes arose, Macho (2001) emphasises the difference between hyperplastic and hypertrophic growth as a possible explanation. Most evolutionary changes in body size are hyperplastic changes; that is, changes occurring early in development and resulting in a linked and consistent pattern of change between two of more features (i.e. brain and body size; Macho 2001). Macho (2001) suggests, however, body size growth in the gorilla may be hypertrophic. In this situation, brain growth and somatic development, for example, are dissociated (Macho 2001). As *Theropithecus oswaldi* is extinct and the gorilla is endangered, Macho (2001) suggests the possibility that change in this manner is unsustainable. This may need to be taken into account when investigating questions regarding early hominins, such as the *P.*, that may also have changed in this fashion (Macho 2001). Similar to issues highlighted by Ross (1998) when assessing the relationship between brain/body mass and broad life-history patterns, predictive models appear to deviate when applied to a certain brain/body mass ratios.

In addition to odontogenetic pattern and timing correlating with broad scale life-history characteristics, it is possible to specifically identify life events using dental microstructure (Bromage & Dean 1985). This allows for histological examination of dental remains to be used for the interpretation of age and odontogenetic timing specific to the individual. As group comparisons and living observation is not possible when studying extinct individuals, a histology-based methodology would remove the need for certain behavioural assumptions necessary for the application of extant analogues. Also, direct assessment of histology of individuals avoids issues that have become evident in regards to brain and body mass scaling. The assumption underlying this method is that cross-striations between long-period incremental growth markers are consistent within

teeth and within all teeth belonging to a single individual (FitzGerald 1998). This was tested through a study of 158 anterior teeth sampled from three modern human populations (FitzGerald 1998). Statistical analysis validated the hypothesis and indicated that histological interpretation is a reliable methodology (Fitzgerald 1998). This histological method allowed a finer resolution of developmental timing to be examined. For example, Reid et al. (1998) also found chimpanzees to have a greatly reduced root formation period before eruption than in modern humans. In fact, it was determined that the major differences in dental development between these two species lie in the first period of root formation rather than the total period of crown formation (Reid et al. 1998). Fine-grained, individual-based methods such as this create the potential for dental development patterns of fossil hominins to be determined without the reliance on modern analogues or the potential hindrance of poorly understood factors such as rate of encephalisation and length of the juvenile period in these species.

A reliable method of histological interpretation also eased the growing concerns regarding the accuracy of radiograph-based studies that were arising at the time (Reid et al. 1998). Reid et al. (1998) supported the use of histological methods, arguing that crown formation times determined through examination of radiographs, were consistently lower than those found through histological analysis. When assessing studies conducted prior to the application of histological methods, the potential for inaccuracy and large error margins must be taken into account.

For the purposes of determining histological markers of specific stressful life events and so making the examination of hypoplastic pits or lines in fossil dentition useful, Schwartz et al. (2006) closely studied a juvenile female gorilla. As this individual was captive-born, all potential life events, both physiological and psychological, as well as factors such as age at each event, sex, and age at death, were known values (Schwartz et al. 2006). By examining short and long-period incremental formation lines in both dentine and enamel, the effects of these events were recorded (Schwartz et al. 2006). This study found major stress lines evident linking closely to events such as surgical procedures (Schwartz et al. 2006). This data suggests that physically traumatic events during the

developmental period would be recorded within the dental microstructure. Schwartz et al. (2006) also reported an accelerated rate of dental development compared to both chimpanzee and other gorilla data, although the potential of the 'wild effect' (per Zihlman et al. 2004; see section 2.2.1.4) is not discussed.

Histology-based methodologies are crucial due to both the ability to identify fine-grain life events as opposed to broad scale life-history interpretations, as well as the applicability to fossil remains. As these methodologies can be applied independent of comparative data or extant analogues, life events specific to the fossilised individual under examination can be identified. This opens up the possibility of not only a more accurate understanding of fossil taxa but also the detection of changes and variability within a species or population due to temporally fluctuating adaptive pressures.

2.2.1.4 Environmental Pressures and Diet and Life-History
As histological markers of odontogenesis have shown to be sensitive to life events, it is important to understand any external variables that may potentially be reflected in this way. Along the lines of the Schwartz et al. (2006) study, assessment of the impact of factors such as trauma or abrupt changes in environment was undertaken through a study of European children sampled in the late 1990's (Zanolli et al. 2011). Differences in neonatal line thickness was examined between three groups: normal delivery, caesarean birth, and operative birth (Zanolli et al. 2011). It was hypothesised that abrupt environmental and dietary changes experienced after birth, the trauma of the birth itself, and the occurrence of hypocalcaemia would lead to distinct differences in the manifestation of the neonatal line (a hypoplastic stress line manifesting at birth; Zanolli et al. 2011). This hypothesis was not supported however, and instead it was suggested that while environmental factors do not have any great effect on the neonatal line, manifestation is related to gestational length (Zanolli et al. 2011). This consistency across environments and correlation with the life-history characteristic of gestational length supports the use of dentition, and specifically dental microstructure, for the interpretation of life-histories.

Diet, however, may impact odontogeny and dental microstructure whereas the trauma and abrupt environmental changes brought on by birth do not. By examining length of formation in each cusp, Reid et al. (1998) hypothesised a link between occlusal morphology and tooth function. Specifically, functional cusps have thicker enamel than non-functional cusps and so take longer to form (Reid et al. 1998). By extension, formation times can help elucidate dietary habits through interpretation of element function and importance of element.

Differences in odontogenetic timing in wild populations versus captive populations of the same species also have implications for the effect of diet and environment on life-histories (Phillips-Conroy & Jolly 1988). Through comparative study of yellow baboons (*Papio cynocephalus*), Phillips-Conroy and Jolly (1988) concluded that all teeth of wild individuals were delayed in relation to captive individuals, with the greatest time delay estimated at approximately 1.5 years. Findings were compared to dental eruption data of the hamadryas baboon (*Papio hamadryas*; Sigg et al. 1982) and demonstrated that while yellow and hamadryas baboon patterns do not differ significantly from one another, these results held true for both species (Phillips-Conroy & Jolly 1988). It was hypothesised that the reason for such a delay might lie in short-term adaptive plasticity (Phillips-Conroy & Jolly 1988). Specifically, certain individuals or populations may adapt relatively rapidly to varied environmental conditions.

The possibility of rapid adaptation to short-term pressures is important to consider when assessing extinct specimens. Within a very short time a significant acceleration of dental development occurred in captive populations (Phillips-Conroy & Jolly 1988). If early hominins also had the capability of shifting odontogeny rapidly through short-term adaptive plasticity, interpretations drawn from histological studies become limited. When studying the fossil record, research is often limited to small sample sizes. This could create the scenario where, through histological analysis, life-history markers of an unrepresentative sample are inaccurately attributed to a species spanning a wide temporal and geographic range. Additionally, a sample drawn from a single species but on the opposite ends of a temporal range could result in what appears to be a large variation but

in fact is indicative of a change in diet or environment over time. Though this presents obvious problems in the application of histological methods for odontogenetic and life-history interpretations, when studies are constrained to specific temporal or geographic samples, such as the Drimolen palaeo-population, the ability to interpret intra-specific variation across these two dimensions arises. Additionally, histological evaluation is exceedingly useful when determining an individual's age at death for demographic interpretation as it is specific to the specimen and does not rely on extant analogues.

2.2.2 Life-History Characteristics of Extant Hominids

The determination of extinct life-histories relies heavily on predictive modelling based on extant patterns. While the employment of histological methods for interpreting odontogenesis limit this necessity, they are not eliminated entirely. For example, as with Smith et al.'s (2015) work (discussed in more detail in Chapter 3), age at death interpretations are calculated histologically but based on the assumption that M1 formation begins at the time of birth as is the case in extant primates. Implications of histologically determined odontogenetic patterns are also interpreted through the lens of extant primates. For these reasons, it must be made clear what an 'extant analogue' or a 'great ape model' refers to. Particularly because the concept of a homogenous developmental model based on great apes is meaningless. As will be discussed in detail, the extant members of this group do not hold to a single developmental model.

As life-history characteristics reflect development, which is in turn dictated by morphology and produces different behaviours, different species have different life-histories. There are, however, baseline patterns at an order, family, or genus level. Broad life-history characteristics seem to hold true across all mammals. When comparing life-histories, however, both pattern and rate must be considered. Two species may, for example, have equivalent molar crown formation times but a different eruption order. Or, as more factors are examined, a correlation between brain growth and dental eruption may exist in both species, but the correlations have different implications.

2.2.2.1 Order Primates

Due to phylogenetic relatedness, patterns that apply to all extant members of the Order Primates can be reasonably assumed to apply to extinct members of the lineage. Godfrey et al. (2001) studied the correlation of variation in dental development across the Order Primates. This included eruption stage at weaning and all life-history milestones, dental patterns of folivores as compared to frugivores, and the adaptive significance of these variations (Godfrey et al. 2001). The results demonstrated folivorous species exhibit an absolutely more rapid pattern of dental development than frugivores as well as a more advanced stage of development at weaning (Godfrey et al. 2001). This study also indicated the importance of brain rather than body size as a tool for predicting dental development, both relative and absolute (Godfrey et al. 2001). Godfrey et al. (2001) put forward dietary hypotheses reliant on foraging independence and food processing by way of an explanation for this pattern. While foraging independence is linked to the length of time a juvenile is reliant on the mother and may be detected through identification of the neonatal line, the functional hypotheses put forward by Leigh et al. (1994) must also be considered as differential diets will result in different dental requirements. That is, if an individual is required to process tough fibrous food immediately after weaning, a higher importance would be put on grinding teeth rather than slicing teeth in individuals whose diet consists primarily of fruit.

Variation in the age at which dentition is required to come into functional occlusion can be interpreted based on the age at which individuals reach certain developmental markers. Age at crown completion does not necessarily dictate age at eruption as the delay between crown formation and gingival emergence varies between species (Kuykendall et al. 1992). Root extension, however, is more consistent with the beginning of eruption. Dean and Vesey (2008) studied root extension rate and timing of modern humans and great apes. This study sampled incisors, canines, and molars of 93 *Homo sapiens*, 53 *Pan troglodytes*, and a combined population of 51 *Gorilla* and *Pongo* (Dean & Vesey 2008). In regards to anterior teeth, modern humans displayed a far more regular pattern of increase than the great apes, with chimpanzees in particular showing a short period of rapid growth that then tapered off (Dean & Vesey 2008). Molar teeth in all four

species grew nonlinearly (Dean & Vesey 2008). In regards to overall rate, modern human dentition formed the slowest followed most closely by the chimpanzees, with the gorilla and orangutan sample showing notably faster formation (Dean & Vesey 2008). Dean & Vesey (2008) also report variation in formation rate and pattern between tooth types. This disparity may indicate the importance of a specific dental element to the particular species. Reliance on the mother or functional aspects dictated by diet and masticatory requirements can increase or decrease the importance of particular dental elements. The identification of these patterns can be used in conjunction with life-history characteristics to interpret juvenile behaviours specific to a species or population.

Following this line of argument, Bronikowski et al. (2011) examined senescence across the Order Primates. Variables related to senescence that were tested include longevity and the increase and decrease of mortality rates dependent on age and sex. The sample included one Madagascan prosimian, two New World monkeys, two Old World monkeys, two great apes, and modern humans (Bronikowski et al. 2011). Comparative studies indicated that these variables in modern humans fell within the expected pattern of all other primates (Bronikowski et al. 2011). Across all primates, male mortality rates are tightly dependent on age while female mortality rates are more consistent at all ages (Bronikowski et al. 2011). Due to the spiking in male mortality at certain ages, females also have longer lifespans than males (Bronikowski et al. 2011). Bronikowski et al. (2011) concluded that the pattern of sex and age dependent mortality rates do not reflect phylogenetic relationships but may be influenced instead by behavioural responses to localised selective pressures. That said, patterns that can be shown to be consistent across the Order Primates can more reliably be applied to interpretation of extinct primate taxa.

2.2.2.2 Modern Humans

As most early hominins are hypothesised to be ancestral to the lineage of modern humans, developmental patterns of *Homo sapiens* have been used as interpretive models for fossil hominin species. Recent modern human dental development patterns were identified first for aging and utilised later for life-history interpretation. Early works in determining the odontogeny of modern *H. sapiens* often focused on small and biased

samples. Specimens examined in these studies were frequently sourced through hospitals resulting in a sample of pathological juveniles (Gleiser & Hunt 1955; Moorrees et al. 1963). These pathologies likely affected the odontogeny of the individuals. Additionally, many of the standard dental development patterns for modern humans were established in the early to mid 1900s (Massler & Schour 1941; Clements et al. 1953; Miles 1958; Moorrees et al. 1963; and others). It is possible, if not likely, that these patterns vary somewhat from the true pattern of the current population of *H. sapiens,* as environmental pressures and diet appear to play a significant role in odontogeny. Thirdly, these patterns sampled only 'Caucasian' individuals living in England or America, further biasing the results.

2.2.2.3 Great Apes

Since the early 1900's, it has been hypothesised that the early hominin development resembled either modern humans or great apes; each with varying, often alternating, support (discussed and cited in detail below). As with modern human analogues, great ape analogues prove problematic. A primary issue concerns the assumption that there is a homogenous great ape developmental pattern. While broad patterns can apply to all great apes, as with all primates, fine-grained life-history characteristics are influenced by variables specific to the adaptive strategies and behaviours of individual species. Additionally, errors in early studies led to false conclusions concerning ontogenesis of great ape species. These studies rely either on observation of wild or captive ape individuals or assessment of deceased individuals. Methods for the former have improved through the years and so have the reliability of the results. Though the application of great ape analogues to extinct hominin species yield erroneous results (see discussion in this chapter and Chapter 3), the approaches and techniques developed through the study of great ape life-history and odontogenesis are crucial to the interpretation of that of extinct taxa. Additionally, correlations between and variability within life-history characteristics determined through these studies become integral in the interpretation of fossil hominin species.

As brain mass and development is thought by some to indicate broad life-history patterns, this was the starting point for many early studies. Early in the study of hominid life-histories, it was thought that great ape brain growth could not be correlated with odontogenesis as adult cranial capacity was reached by one year of age, before the loss of the deciduous teeth (Macnamara 1902; Keith 1910; Duckworth 1915). However, Zuckerman's (1928) study seemed to indicate the exact opposite. His work indicated that the rate of cranial growth after the eruption of M1 could be used to determine the sex of the individual by showing marked dimorphism, while cranial capacity before the age of M1 eruption was nearly indistinguishable between sexes (Zuckerman 1928). In this study, Zuckerman (1928) also determined that brain growth continues until the period between M2 eruption and M3 eruption. Zuckerman (1928) found chimpanzee brain growth after M1 eruption is almost twice that which would be expected in modern humans. In regards to dental development, however, the study suggested that the duration of the tooth stages themselves, both formation and eruption, were equivalent in chimpanzees and modern human (Zuckerman 1928). This conclusion of equivalent odontogenesis in modern humans and their closest living relative, the chimpanzee, led to the early assumption that extinct hominins would have displayed an identical odontogenetic pattern, as well.

The chimpanzee odontogenesis implied by Zucherman's (1928) study was later challenged and falsified; Nissen and Riesen (1964) demonstrate that chimpanzees appear to mature at three times the rate of modern humans. Their sample comprised of 16 laboratory-born chimpanzees, although the final analysis was based on only 15 of the individuals (Nissen & Riesen 1964). Documented ages of each tooth gained and lost were compared against both modern human and *Macaca mulatta*, the rhesus macaque used to represent Old World monkeys (Nissen & Riesen 1964). The study found little sexual dimorphism in the chimpanzee sample, an eruption sequence matching that of the male rhesus macaque, and an overall maturation rate just more than twice the rhesus macaque (Nissen & Riesen 1964). This conclusion is suggestive of closer developmental similarities between non-human great apes and Old World monkeys than even non-human great apes and modern humans. This scenario highlights the disparity between an

interpretation of early hominins based on a great ape model and an interpretation based on a modern human model.

In an attempt to capture a more extensive picture of chimpanzee dental emergence, Conroy and Mahoney (1991) conducted a mixed longitudinal study of 58 individuals, 22 males and 36 females, over a ten-year period. This study examined both deciduous and permanent teeth, sexual dimorphism, and possible differences between mandibular versus maxillary and antimere eruption (Conroy & Mahoney 1991). While results showed most permanent dentition was highly coordinated despite the above-mentioned factors, three element pairs deviated from this model: RI^2 and RI_2, LI^2 and LI_2, and LM^1 and LM_1 (Conroy & Mahoney 1991). The deciduous teeth were much more variable, with seven elements deviating from the expectant model (Conroy & Mahoney 1991). In contrast to Nissen and Riesen's (1964) study, which stated a lack of statistically significant sexual dimorphism, Conroy and Mahoney's (1991) results suggest earlier emergence ages for females than males. Also and in all cases, there appeared to be a significant lag time between M1 and I1 emergence (Conroy & Mahoney 1991). By way of explaining these variances, eight sequence polymorphisms were proposed (Conroy & Mahoney 1991). Problematically, eight varying polymorphisms of odontogeny in chimpanzees make the application of a chimpanzee analogue to extinct taxa meaningless for interpretive purposes.

Supplementing the study conducted by Conroy and Mahoney (1991), Kuykendall et al. (1992) conducted a probit and survival analysis of tooth emergence on the same mixed-longitudinal sample of 58 chimpanzees. This study used between-group comparisons to identify median emergence ages, standard ranges of variability, and a set emergence sequence for deciduous and permanent teeth (Kuykendall et al. 1992). While no statistically significant differences were found between antimeres or mandibular versus maxillary dentition, differences were identified between males and females (Kuykendall et al. 1992). Male chimpanzees within this sample were found to consistently achieve eruption of a number of teeth significantly later than females (Kuykendall et al. 1992). The issue of sexual dimorphism further complicates the application of these models to

extinct taxa. As sex is often difficult to determine in fossil individuals and degree of sexual dimorphism within species is often unknown, the presence of sexually dimorphic dental development is problematic for non-histological assessment. That said, the lack of statistically significant variation between mandibular and maxillary dentition is advantageous for odontogenetic interpretation.

With the aim of gaining comparative knowledge, Aiello et al. (1991) examined 35 great apes between the ages of six months and five years through direct observation. In this study, gorillas were found to show much greater wear than both chimpanzees and orangutans at all stages of life (Aiello et al. 1991). It was hypothesised that instead of being related to enamel thickness, eruption sequence, cuspal morphology, and duration of occlusal attrition, these results indicated differences in age at weaning and/or diet (Aiello et al. 1991). It was noted that there was no significant difference between the chimpanzee sample and the orangutan sample at any age (Aiello et al. 1991). If differential wear is related to diet and age at weaning, the identification of the neonatal line in fossil dentition in conjunction with isotopic studies would assist in wear pattern identification and functional significance.

The work of Hill et al. (2001) aimed to create a composite life table for free-living (wild) chimpanzees. This thorough work combined data sets from five different study populations: Gombe, Tai, Kibale, Mahale, and Bossou (Hill et al. 2001). The compiled information resulted in a few distinct patterns emerging. On average, males show a higher mortality rate than females (Hill et al. 2001). This is likely related to higher risks for males in the chimpanzee behavioural regime. The average life expectancy at birth was found to be 15 years and risk of death due to "risk taking behaviours" was highest at this age, though some individuals lived well into their forties (Hill et al. 2001). Some inter-site variability in mortality data was found, however the differences were not significant (Hill et al. 2001). Comparatively, modern human foragers show a lower rate of morality in the young adult years (Hill et al. 2001). Hill et al. (2001) suggests this pattern may be linked to the longer juvenile period of modern humans. It is this recent and thorough

report that is applied later in this study for the purposes of comparative demographic interpretation (Chapter 7).

More recently, Machanda et al. (2015) addressed environmental effects on dental eruption patterns in *Pan troglodytes*. By studying living, wild-captured, known-age individuals from the Kibale National Park, Machanda et al. (2015) examined the 'wild effect' (per Zihlman et al. 2004) in east African chimpanzee populations. Over a three-year period, high-resolution photographs of the dentition of this population were studied for the purposes of creating a comprehensive dental eruption pattern (Machanda et al. 2015). It was found that dental emergence ages of the Kibale chimpanzees were similar to those of both the Gombe live-captured wild chimpanzees and the Tai Forest deceased wild chimpanzees (Machanda et al. 2015). This larger sample was then used to represent wild chimpanzee dental eruption patterns (Machanda et al. 2015). Machanda et al. (2015) determined that deciduous and M1 'early-emerging teeth', which appear during maternal dependence, are indistinguishable from captive chimpanzees. Later forming teeth appear much later in life in wild populations, and only slightly overlapping with the upper age boundary of captive chimpanzees (Machanda et al. 2015).

Within the Kibale wild chimpanzee sample, considerable variation was observed (Machanda et al. 2015). Dental emergence did not appear to consistently correlate with maturation milestones such as age at weaning or age at first female reproduction (Machanda et al. 2015). Contrary to previous studies, Machanda et al. (2015) concluded that there is a low correlation between odontogenetic pattern and life-history in chimpanzees due to the aforementioned variation. If this hypothesis is supported, contrary to decades of previous study, it may be that not only is the application of extant models to extinct taxa invalid but the use of odontogeny to interpret life-history may also be invalid. If this were the case, direct histological examination of dental development would represent the least biased approach to odontogenetic, life-history, and age at death interpretation of early hominin populations.

Earlier studies had suggested the use of histological growth markers for the interpretation of odontogeny. Beynon et al. (1991) expanded on earlier comparative work by studying dental development in both the gorilla (*Gorilla gorilla*) and the orangutan (*Pongo pygmaeus*). This study critically assessed the use of radiographs in cross-sectional studies, (and in particular Dean and Wood 1981), to interpret odontogenetic patterns and consequently suggested the use of histological methods (Beynon et al. 1991). Instead of radiographic imaging of known or estimated-age individuals, Beynon et al. (1991) used incremental growth lines formed through regular enamel deposition during the formation period of the tooth.

Crown formation times in individual teeth were estimated and used in conjunction with the incremental growth lines to develop a full chronology for dental development in these two species (Beynon et al. 1991). These results showed previous work accurately identified P4 through M3 chronology and sequence in great apes (Beynon et al. 1991). However, I1 through P3 crown formation timing was found to be significantly underestimated in radiographic studies (Beynon et al. 1991). Beynon, et al. (1991) concluded that while overall dental development periods in great apes are much shorter than that of the modern humans, the anterior teeth of the great apes take significantly longer to form. This pattern is perhaps reflective of the importance of different dental elements to the species' adaptive strategies and so must be considered when assessing extinct taxa. In regards to root extension, gorilla rates were found to be fast (~13µm/day) and may be associated with early tooth eruption (Beynon et al. 1991). The study of incremental growth lines as opposed to gross observation of dental development allows for a finer-grained and individual-specific odontogenetic interpretation; something required for accurate interpretation of life-history characteristics such as age at weaning.

Techniques used in histological interpretation have improved in more recent studies. Identifying a problem with intraspecific variation in previous histology-based studies, Smith et al. (2007) examined molar development in chimpanzees. In addition, Smith et al. (2007) criticised previous studies for not taking account of the time required for root formation during the delay between alveolar and gingival emergence. In order for dental

development patterns of chimpanzees to be a useful interpretive tool, these factors must be taken into account.

This study examined daily secretion rates between cusps, cusp types, and molars and found them to be consistent (Smith et al. 2007). This is particularly advantageous as many fossil individuals consist of isolated dental elements. The number of Retzius lines and cuspal thickness, however, both vary across these three areas resulting in significant variation in formation times throughout the dentition (Smith et al. 2007). Enamel depositional periodicity was determined to be approximately six to seven days and formation time required increased from inner to outer cuspal enamel (Smith et al. 2007). While cuspal initiation and completion sequences were found to vary, mandibular molars were more consistent (Smith et al. 2007). The former was found to range from approximately two to three years, increasing overall from M1 to M2, and decreasing overall from M2 to M3 (Smith et al. 2007).

Given that is has been demonstrated that each of the great ape species display a unique pattern of odontogeny and life-history, the proposal of a homogenous 'great ape model' has been shown to be invalid. Additionally, as a species' behaviours, such as a longer time of dependence on the mother, appear to influence odontogeny and life-history, dental development cannot be used in all cases to predict life-history characteristics. As this is the case, histological studies that directly assess the development of an individual are far more reliable for these interpretations. Consequently, an overarching 'great ape model' cannot be applied as an interpretive analogue for extinct hominin species.

2.2.2.4 Papionins

In the case of certain early hominins, such as *P. robustus*, it has been suggested that extant baboons may in fact represent the best behavioural model (Washburn & DeVore 1961; Jolly 1970). This would imply that interpretations of behavioural-dependant life-history characteristics may be interpreted through this behavioural analogue. While, of course, comparisons such as these are not without their faults, a behavioural comparison may be more reliable than a strict developmental comparison for the reasons outlined

above. Problematically, behaviours cannot be observed in extinct populations and can only be interpreted by proxy through developmental and anatomical characteristics.

In addition to individual or sex based variability, significant differences have been documented between related papionin species despite similar adaptive strategies. Kuhambu and Eley (1991) examined 95 wild olive baboons (*Papio anubis*) aged 2 to 102 months. Data collected from this wild population sample was compared to both wild and captive-born yellow baboons (Kuhambu & Eley 1991). As for the emergence pattern as a whole, timing did not appear consistent across all dental elements. The first molar and both incisors of wild olive baboons come into gingival emergence earlier than wild yellow baboons and resemble captive yellow baboons closely (Kuhambu & Eley 1991). Later emerging teeth in wild olive baboons however, were significantly delayed compared to captive yellow baboons, instead resembling the timing of the wild sample (Kuhambu & Eley 1991). Significant sexual dimorphism was recorded for the wild olive baboons and there was considerable variation among male individuals in regards to these later emerging teeth (Kuhambu & Eley 1991). Overall, Kuhambu and Eley (1991) concluded dental emergence timing is consistent between wild baboon species, or subspecies, while full permanent dentition acquisition in all wild populations can be up to one year later than captive populations (Kuhambu & Eley 1991). Kuhambu and Eley (1991) recommend the use of dental development data for aging, however caution was urged as significant individual variation suggests that the use of isolated dental elements is not reliable. In contradiction to the conclusions put forward by Smith et al. (2007), this assertion presents a serious problem when assessing fossil material as the majority of the fossil record consists of isolated dental material. It is possible that this disparity has to do with either inter-specific variation or a disconnect between formation patterns and eruption patterns.

2.2.3 Interpretations of Extinct Hominin Taxa

Until the early 2000's, most if not all studies assessed life-history patterns through direct comparison with extant primate species. As previously discussed, early researchers believed early hominins would have exhibited an ontogenetic profile and life-history

pattern of either extant great apes or modern humans (as discussed above; see, for instance, Smith 1991). This concept is unsupported on multiple accounts. This approach assumed a linear progression from something equivalent to an extant ape to modern human. Not only is it unlikely for this evolution to have been strictly linear, it cannot be assumed that the last common ancestor (LCA) would have exhibited life-history and developmental patterns equivalent to extant apes.

Furthermore, a homogenous great ape pattern does not exist as it has been demonstrated that each species within this group exhibits a unique pattern of development and life-history. Studies discussed within the previous sections outline this disparity. It has been hypothesised that life-history and developmental patterns are influenced most heavily by the adaptive strategy and behaviours of the species in question (Bronikowski et al. 2010). Following this, it is unsurprising that neither the gorilla, the orangutan, nor the chimpanzee exhibit equivalent life-histories.

This, of course, should also hold true for early hominin species (Smith et al. 2015). This is an additional issue with the concept of applying extant comparative analogues to extinct species. In many early studies, hominins are discussed in grades such as the 'australopiths'. As the term 'australopith' applied to all *Australopithecus* and all *P.* species spanning millions of years and thousands of kilometres, it is illogical to assume all australopiths would have adhered to the same adaptive strategies.

As these studies progressed, histological methodologies were employed to supplement comparative analogues and, recently, have more or less replaced them. Histological assessment of odontogeny involves examining the microstructure of dental elements for the purposes of interpreting growth patterns. Enamel and dentine are deposited in a regular manner in long- and short- period incremental growth striations (Appendix 1). Life-history markers such as birth and weaning can be determined through identification of irregularities within these striae. Chronological age can be determined as enamel periodicity informs on the length of dental formation. That said, developmental studies conducted on extant primates have been very informative as to the interrelatedness of

particular developmental, morphological, and life-history characteristics. These relationships are important when extrapolating histological results to be applied on a larger scale.

Histological studies, however, have not fully broken away from the flaws of comparative methodologies. While earlier studies would conclude as to whether a particular species or individual exhibited an ape-like or modern human-like developmental pattern, histological studies make these assessments on an element-by-element basis. That is, despite not having to employ an extant analogue, results are still discussed in these binary terms.

Additionally, histological methodologies do require extant-based assumptions. For example, Smith et al. (2015) assessed the internal dental microstructure of a number of hominin individuals to determine ages at death. This method used known periodicities to determine chronological age based on long-period striae counts. This, however, will determine only the length of time the specific element in question has been developing and so can only be applied to individuals at a specific developmental stage. Once the element has completed crown formation, this method has no way of determining the passage of time. Additionally, the point at which formation begins must be assumed. In Smith et al.'s (2015) study, it is assumed that the first permanent molar begins at birth, as is the case in modern humans. While histological methods limit the need to rely on extant models, they do not eliminate it.

2.2.3.1 Comparative Interpretation

Body mass, brain mass, and odontogenetic correlations with life-histories of extant primates have been used as analogues for interpreting life-histories of extinct hominins. For example, using chimpanzee dental and brain development data collected in his study, Zuckerman (1928) aged Taung 1 at 6-7 years of age with an expected adult cranial capacity of 540.5cc. This specimen has also been aged to 5.5-7.5 years using comparative models (Mann 1975), while histological methods have aged the Taung child at 3.73-3.93 years (Lacruz et al. 2005). These inconsistencies are due to the previously discussed

faults in comparative modelling. The similarities between the Zuckerman (1928) and Mann (1975) ages are indicative of the problem as the former applied a chimpanzee analogue and the latter applied a modern human analogue. As it is known that chimpanzees develop approximately twice as fast as modern humans, the fact that these two studies concluded nearly identical ages exemplifies how ill fit extant patterns are to extinct development.

While broad patterns, such as those discussed above, may apply to extinct species, precise life-history and developmental patterns cannot be determined through the application of extant analogues. Many studies that applied comparative methods have been disputed or disproven. However, despite many of these conclusions being incorrect, these early studies did help to elucidate some of the causal factors and mechanisms behind the evolution of life-history and general developmental patterns. It has been hypothesised that a change in life-history variables is caused by a change in adaptive strategy and related variables such as behaviours (Bronikowski et al. 2011), element function (Reid et al. 1998), and element importance (Dean & Vesey 2008). Correlations such as these are crucial for the interpretation of life-history characteristics and developmental markers identified later by histological studies.

Despite the fact that improved radiographic technology has allowed for finer grained assessment of dental morphology, the necessity of comparing extinct specimens to extant analogues has not been overcome. Rather, technological advances have highlighted that extinct hominin species do not universally adhere to the dental developmental pattern of a single extant primate. For instance, despite concluding that both *P.* and *Australopithecus* evince an 'ape-like' pattern of odontogenesis in general, Bromage (1987) notes that certain dental elements belonging to *P.* actually grouped developmentally with modern humans. In other words, Bromage's (1987) consequent application of a 'great-ape' model to *P.,* notwithstanding similarities to modern human, is likely to be erroneous. However, Bromage's (1987) study does serve to highlight the importance of assessing the entire dental array of extinct hominins, and the strong likelihood that extinct species adhered to dental development patterns that were irrevocably distinct from extant analogues.

It is critical to note that this study asserted a hypothesis that did not refer to odontogeny as a whole. Bromage (1987) proposed that while *Australopithecus* displayed an ape-like odontogenesis, *P.* incisors departed from this model and displayed a modern human-like odontogenesis, if only superficially. While the concept of applying either of these extant models to extinct taxa is no longer supported (discussed below), this hypothesis highlights a key issue with extinct odontogenetic interpretation. As clarified by later studies, differential importance of dental elements (Dean & Vesey 2008) and differences in elemental functionality (Reid et al. 1998) can influence odontogeny at a level too fine-grained to be discussed by broad, overarching patterns. Distinctions such as these are critical to understanding not only odontogeny in extinct hominin taxa, but also life-histories and behavioural patterns.

Conroy (1988) reviewed the sequential studies assessing permanent incisor versus molar formation and eruption patterns in *P.* While heavily debated, claims are difficult to test as developing incisors are difficult to visualise using the conventional radiographic imaging available at the time due to the heavy mineralization present in fossilized material (Conroy 1988). Using high-resolution computed tomographic imaging, Conroy (1988) reassessed the hypothesis that while *P.* molars developed in a manner similar to apes, *P.* incisors developed in a manner similar to modern humans. Conroy (1988) conducted an examination of a *P. robustus* specimen, SK 61, from Swartkrans Member 1. Increased resolution helped confirm the hypothesis that the erupted incisors were in fact deciduous and allowed the developing permanent incisors to be studied (Conroy 1988). It was found that the developing I1s showed very little root formation at this stage (Conroy 1988). Conroy (1988) commented that this discovery acts to weaken Broom and Robinson's (1951) hypothesis of M1/I1 eruption pattern synapomorphy between *P.* (robust australopiths) and modern humans.

Again in a later two-part publication, Conroy and Vannier (1991a; 1991b) discussed South African australopith dental development. The first of these publications addressed problems in traditional views of pattern and chronology (Conroy & Vannier 1991a). This

study questioned views that delayed maturation resulting in modern humans taking approximately twice as long to reach adulthood as apes, was already present in australopith species (Conroy & Vannier 1991a). Using 2D and 3D computed tomography, this study inspected theories concerning the chronology and pattern of dental development in these hominins with the aim to identify problems for future research such as intra- versus inter-species variation (Conroy & Vannier 1991a). It was concluded that 'robust' australopith (*P.*) species were more modern human-like in dental development while 'gracile' australopith (*Australopithecus*) species were more ape-like (Conroy & Vannier 1991a). As *P.* is thought to represent a sister taxon to the modern human lineage while *Australopithecus* is thought to represent directly ancestral species, the pattern proposed by Conroy and Vannier (1991a) is not what would be expected. However, it must be considered that these resemblances are only superficial (Bromage 1987) and are not indicative of phylogenetic relationships (Bronikowski et al. 2011).

The results of this approach suggested that while both *P. robustus* and *Australopithecus africanus* may have had a relatively rapid odontogenetic *rate* (rate of crown development, root extension, delay between formation and eruption, eruption time, and delay between element eruption), significant differences in *pattern* were likely present (Conroy & Vannier 1991b). Aiello et al. (1991) theorised that *P.* more closely resembled patterns observed in the gorilla, and that this may reflect short interbirth intervals and faster reproductive rates than both earlier and later hominids. A species displaying an odontogenetic profile similar to both the gorilla (postcanine dentition) and modern human (incisors; Bromage 1987), supports the hypothesis that function (Reid et al. 1998) and behaviours influence development and life-history far more than phylogeny (Bronikowski et al. 2011).

As behaviours appear to play a larger role than phylogenetic relatedness in odontogeny and life-history (Bronikowski et al. 2011), the application of extant analogues for interpretation of adaptive strategy may be far more useful than the confused application of extant analogues for identification of developmental patterns. Using the Taung Child (Taung 1) as a representative of the problem, Smith (1992) examined when, how, and

why modern human life-history evolved and how life-history evolution may be reflected in fossil species. By applying allometric models to this specimen, Smith (1992) studied the rate and pattern of dental maturation. The relationship between these factors was then assessed through examination of sexual maturity versus somatic maturity in primates and other mammals, dental eruption and replacement in primates, and dental development in the Taung Child, the great apes, and modern humans (Smith 1992).

This comparative study showed three different relationships applying to different suites of life-history variables: Unrelated, Fixed in pattern, and Pattern adjusts with rate or "scale of life" (Smith 1992). The first relationship was found to be rare, limited to the oestrous cycle length and development of one molar in relation to another (Smith 1992). The second result, also rare in mammals, Smith (1992) argues is the most useful, providing an opportunity to determine chronological age. The third result, described as allochrony, is the most common in primates (Smith 1992). This situation relates to an earlier-discussed theory correlating slow growth with certain life-history variables related to a longer life, and fast growth reflecting the same for a shorter life (Ross 1998). With these interpretations in mind, Smith (1992) concluded that the developmental patterns seen in the Taung child are characteristic of the latter 'live-fast, die-young' category (Ross 1998), rather than the modern human pattern. Smith (1992) also suggested that the pattern of life in australopith species does not reflect that of modern humans because the life-histories of these early hominins were not divided into the same proportions. Though the proposal of three suites of life-history variables can clarify the interpretation of extinct hominin patterns, it also creates an additional layer of complexity. Different variables within a single species adhering to a different suite as proposed by Smith (1992) may explain the confounding conclusions of previous studies.

By examining two life-history variables commonly thought to correlate well—cranial capacity and age at M1 eruption—Smith et al. (1995) interpreted ontogeny for both the australopiths and early *Homo* (*H. habilis* and *H. erectus sensu lato*). Smith et al. (1995) first defined a clear distinction between cranial capacity, brain weight, and brain volume; terms that had been used synonymously up to this point. Smith et al. (1995) assessed the

effect of changes in confidence intervals and standard deviations, and also ensured an appropriate sample of modern humans for statistical comparison was used. These were areas that Smith et al. (1995) were highly critical of in previous works. Published literature on the topic of anthropoid dentition was then re-examined (Smith et al. 1995).

The results of this study suggested a great ape-like dental eruption pattern rather than modern human-like for australopiths species, while early *Homo* specimens seemed to display an intermediate maturation rate (Smith et al. 1995). These results, and those in regards to the brain size/molar eruption relationship, were said to differ greatly from previous work (Smith et al. 1995). Smith et al. (1995) concluded a definite correlation between brain size and M1 (particularly M_1) eruption and hypothesised a link between this correlation and extended maturation. A conclusion such as this is more in line with adaptive strategy and behaviour as the primary influential factor for life-history and odontogenetic change as extended maturation is indicative of a distinct behavioural suite (Kaplan et al. 2000).

Subsequent comparative studies, combined with advancing methods of bone and dental development research, indicated that the modern human pattern of life-history is dependant on rich energy sources and low mortality (Smith & Tompkins 1995). It was also found that overall patterns of growth, maturation, and aging evolved in parallel with brain size (Smith & Tompkins 1995). Using these new techniques, Smith and Tompkins (1995) assessed the evolution of life-histories through the Family Hominidae. It supported the hypothesis that the australopiths more closely resembled the great apes rather than modern humans (Smith & Tompkins 1995). Assessing life-histories within the *Homo* lineage in more depth than the previous Smith et al. (1995) study, *Homo erectus* was found to have a life-history unlike any living hominoid, displaying instead a unique combination of a faster developmental rate than modern humans, the lack of an adolescent increase in developmental rate, and infants more helpless than that of the chimpanzee yet less helpless than that of modern humans (Smith & Tompkins 1995). This transitional state, however, did not seem to be present at the beginning of the genus

as early *Homo* specimens were not found to display these traits (Smith & Tompkins 1995).

Immediately, this apparent trajectory seems in contradiction to assertions that life-history change is influenced by adaptive strategy and not by phylogenetic relatedness. The idea that species within a genus would have had similar adaptive strategies is however, supported almost by definition. Indeed, Wood and Collard (1999) take this principle a step further by suggesting that a shared adaptive strategy be a criteria for inclusion of distinct species within the genus *Homo*. It would then be a fair assumption that the apparent movement of life-history patterns in a particular direction would be indicative of species within the genus *Homo* displaying an intensified adaptive strategy through time.

One recurring distinction between both extant apes and modern humans, as well as proposed between australopiths and *Homo,* life-history patterns, is delayed maturation and its implications for more advanced cognition (Kaplan et al. 2000). Conroy and Kuykendall (1995) examined delayed maturation and its assumed correlation with tool making as a result of the need for time to learn complex skills. Through a study of tool use and development in South African early hominins, no evidence of this association was found (Conroy & Kuykendall 1995). These results led Conroy and Kuykendall (1995) to question the assumption that delayed maturation is associated with the need for an extended period of dependency in childhood, cooperative hunting, food sharing, sexual division of labour and other related behaviours. It was suggested that the evolutionary pressures driving delayed maturation may not have appeared until after the australopiths (Conroy & Kuykendall 1995). The purely functional proposition for delayed maturation is an adaption to accommodate the birth of increasingly large-brained individuals. If encephalisation, and so brain mass, increase is at all gradual along the evolutionary lineage to modern humans, the equally gradual extension of childhood to accommodate postnatal brain growth may, for a period, be undetectable within the fossil record.

Zihlman et al. (2004) further addressed the previously discussed 'wild effect' and resultant implications for life-history interpretations of fossil hominins. Disparity between life-histories and developmental patterns of captive versus wild chimpanzees have direct implications on the effect of adaptive strategy on these variables. This study compared ontogenetic information on chimpanzee populations from three different African sites: Gombe, Tai, and Bossou (Zihlman et al. 2004). Alveolar emergence data collected was used to estimate gingival emergence ages so all data would be comparable (Zihlman et al. 2004). The resultant comparison showed permanent dentition in wild chimpanzees erupted later than 90% of captive chimpanzees (Zihlman et al. 2004). As molar eruption is believed by many to correlate strongly with certain life-history variables, Zihlman et al. (2004) hypothesised that delay or acceleration of these events can be interpreted. Following this line of reasoning, it was suggested that information regarding fossil hominins could be gathered in this way (Zihlman et al. 2004). Indeed, Zihlman et al. (2004) put forward the theory that *Homo erectus sensu lato* perhaps had a life-history schedule similar to wild chimpanzees. This would be a unique instance of homoplasy, as the chimpanzee is likely no more similar to the hominin's LCA than modern humans and it has been suggested on anatomical grounds that *Homo erectus* is similar to anatomically modern *Homo sapiens* (Leakey & Lewin 1993). Additionally, if life-history is reliant on adaptive strategy, it seems unlikely that a more derived, tool using (Leakey et al. 1964), and possibly fire using (Wuethrich 1998) hominin would resemble the chimpanzee.

With Zihlman et al. (2004) in mind, Smith and Boesch (2011) further investigated the effects of the 'wild effect' on fossil hominin interpretations. Noting that the difference between wild and captive chimpanzees reported in the Zihlman et al. (2004) study was 1 to 1.3 standard deviations, Smith and Boesch (2011) re-examined the sample and concluded that despite a small sample size and the possibility of error, the 'wild effect' was still present enough to warrant investigation.

This study also considered the possible reasons for the observed differences and the implications for interpreting deceased individuals in the fossil record. Using chimpanzees

as a comparative model, Smith and Boesch (2011) found that poor environmental conditions result in delayed tooth eruption, though it is unclear whether formation times are affected. External factors such as severe environmental pressures can vary from generation to generation, presenting further obstacles to determining species-wide patterns. As it is almost always impossible to determine cause of death in fossil remains, ruling out disease is also problematic. This limitation may in turn bias standard dental development data. The immense variability in extant ape analogues and the inability of the researcher to rule out pathology or taphonomic bias, suggest that direct histological examination of the fossil remains is the most reliable method for interpreting the life-histories of these individuals (Smith & Boesch 2011).

As additional studies suggest an increasing number of variables contributing to life-histories and developmental patterns, it becomes important to examine the evolution of modern human life-histories. Mahoney (2008) examined intraspecific variation in M1 enamel growth in modern humans and discussed its implications for evolution and fossil hominin interpretation. This study sampled 15 unworn LM_1s from juvenile modern humans (Mahoney 2008). Timing, sequence, and enamel thickness were recorded for each of the four cusps (Mahoney 2008). It was found that the protoconid and hypoconid took significantly longer to form than the metaconid and entoconid, though rates within each cusp consistently increased from inner to outer enamel (Mahoney 2008). Similarly to conclusions drawn from the Lacruz et al. (2008) megadontia study, a correlation was noted between variation in enamel thickness and enamel formation variation (Mahoney 2008). As this trend appeared to hold true across several primate species, it appeared possible that this was reflective of a slow evolutionary change towards modern human extended growth (Mahoney 2008).

Robson and Wood (2008), using all previously published data, worked to reconstruct the evolution of hominin life-history from both extant and fossil evidence. Firstly the demographic life-history theory was used to distinguish life-history variables such as weaning, longevity and age at sexual maturity from variables such as body mass, brain growth, and odontogenesis (Robson & Wood 2008). This distinction was made due to the

theory that the latter set of features correlate strongly enough to be utilised in life-history interpretations (Robson & Wood 2008).

Secondly, the study also aimed to identify which traits or variables are likely shared between modern humans and extant apes, and which belong only to the hominin lineage (Robson & Wood 2008). Extant apes exhibit slow life-histories as compared to other members of the Order Primates (Robson & Wood 2008). As modern humans also exhibit slow life-histories, it is assumed here that this is a trait shared between these two groups and so is present in the LCA (Robson & Wood 2008). An exaggeration of this state is seen in modern humans, manifesting as, for example, shortened interbirth intervals and early weaning thought to result from cooperative breeding (Robson & Wood 2008). This trend characterizes a longer life with slow development, likely due to lower mortality rates (Robson & Wood 2008).

Thirdly, Robson and Wood (2008) aimed to test the strength of proposed correlations between three variables and the life-histories of extant apes. The three features assessed were body mass, brain growth, and odontogenesis (Robson & Wood 2008). Contrary to previous studies (see, for instance, Ross 1998), it was found that body mass is the best of these three as a predictor of extant ape life-history (Robson & Wood 2008). The use of both brain growth and dental development in making these interpretations is cautioned and it is asserted that they are only weakly correlated (Robson & Wood 2008).

These results appear to hold true across all hominin data examined in this study (Robson & Wood 2008). In regards to fossil hominin interpretations, it was concluded that while *Homo erectus* displayed mean body mass, adult brain size, and dental formation times consistent with modern human, both the timing and sequence of dental eruption were found to be inconsistent with this pattern (Robson & Wood 2008). *Homo antecessor* was attributed a brain size similar to that of *Homo erectus* but displayed the opposite dental results (Robson & Wood 2008). Both *Homo heidelbergensis* and *Homo neanderthalensis* were also studied and appear to be consistent with modern human life-history results. However, the sample size was too small to confidently make this claim (Robson & Wood

2008). The *P.* clade, uniquely, displayed a pattern of odontogenetic variables that appear to set it apart from both modern human and great apes (Robson & Wood 2008).

Dean (2010) commented that *Pan troglodytes* currently holds the position of the best comparative model for early hominin dental reconstructions. However, he also asserted that further knowledge of the absolute chronological ages associated with developmental landmarks in extinct species must be determined before comparisons of timing and rate during brain growth and dento-skeletal growth could be made (Dean 2010). When it comes to determining these ages, Dean (2010) observed that growth and development of anterior teeth do not appear to be reflective of somatic growth periods while molar teeth have potential in this regard.

Changes in the development of molar teeth best reflect changes in the growth period as a whole (Dean 2010). Earlier ages at molar eruption are interpreted as accelerated life-histories; this manifests as variables such as initiation of earlier mineralisation, more rapid crown formation, and less root present at gingival emergence and beginning of functional occlusion (Dean 2010). Contrary to many previous studies, Dean (2010) asserted that the total period of formation for individual teeth is similar in modern humans and in chimpanzees. Odontogenesis of fossil hominins as a whole exhibit a 'mosaic' of ape-like features, modelling closest to *Pan* though some—particularly megadontic species such as *P.*, for example—may be more similar to *Gorilla* (Dean 2010).

Assertions made by Dean (2010) are somewhat contradictory. That is, it is stated that earlier mineralisation and rapid crown formation are indicative of accelerated life-histories yet the formation times of chimpanzee and modern human dentition are similar (Dean 2010). As it is generally accepted that chimpanzees matures approximately twice as fast as modern humans (Nissen & Riesen 1964) and so does not display a similar life-history, these two assertions are difficult to reconcile. Dean (2010) does, however, note two crucial concepts within this study. Firstly, is the concept of early hominins exhibiting a 'mosaic' of ape- and modern human-like life-history traits. As life-history and

developmental patterns are reflective of adaptive strategy and it cannot logically be assumed that the adaptive strategies of early hominins would be exactly equivalent to any extant species, it follows that variables reliant on these factors would also be disparate. Secondly, the importance of determining exact chronological age through developmental landmarks is highlighted. This approach avoids the application of extant analogues or comparatives for assigning ages to fossil individuals and instead assesses histological markers within the individual's dentition. This concept will be discussed in detail in the following section (2.2.3.2) as histological assessment has become more commonplace.

Modern human history is unique and distinct from all other primates, and is defined by early weaning, extended childhood, late first reproduction, short interbirth intervals, and a long lifespan (Smith et al. 2010). Great apes, on the other hand, exhibit later weaning, earlier first reproduction, and longer interbirth intervals, among other things (Smith et al. 2010). Dental analysis inspecting ontogenesis indicates both australopith and early *Homo* species had a much more rapid ontogenesis than modern human (Smith et al. 2010). The question of when the complete modern human life-history was accrued has been a topic of much discussion. Smith et al. (2010) examined dental evidence from *Homo neanderthalensis* to compare the ontogenesis of this species to that of modern human. It was found that dental formation in *Homo neanderthalensis* was still significantly faster than that of modern humans (Smith et al. 2010). In fact, even Middle Palaeolithic *Homo sapiens* exhibited some differences from modern humans (Smith et al. 2010). Both taxa, however, show significantly extended dental development periods than those seen in earlier hominins (Smith et al. 2010).

Schwartz (2012) investigated the origins of the modern human life-history through a comparative study of extant apes to modern humans and examination of australopith and early *Homo* species. Schwartz (2012) identified three main distinguishing features between modern human and extant ape life-histories: early weaning, extremely short interbirth intervals, and prolonged gestation, growth, and maturation. This study presented three hypothetical beginnings of the development of a modern human life-history: at the base of the hominin lineage radiation (~6 Ma), with the origins of the

genus *Homo* (~2.5 Ma), or significantly later (post ~ 200 ka)—perhaps occurring in *Homo sapiens*, alone (Schwartz 2012).

Schwartz (2012) investigated these possibilities through examination of evidence of the pace of development and maturation of fossil hominins. This study indicates that all hominins likely have slightly varied life-histories affected by the environment, ecology, and specific selective pressures applied to them (Schwartz 2012). A further complication is implied by the fact that while the binary identification of chimpanzee-like or modern human-like appears warranted due to the hominin lineage split, certain hominin species seem to resemble gorilla much more closely (Schwartz 2012). Schwartz (2012) went a step further than the assertion made by Bronikowski et al. (2011) and suggested that factors related to adaptive strategy influence life-histories to a degree great enough to obscure phylogenetic implications. Findings such as these highlight the importance of individual or population based studies such as those utilising histological methodologies as opposed to extant comparative models.

Many of these previous studies address great ape life-histories in a manner that implies they are uniform. Kelley and Schwartz (2012) criticized this practice, asserting that the life-histories of the great apes differ greatly from one another and so cannot be used as a single analogy. It is also stated that the correlation between brain weight and dental development is, contrary to multiple previous studies, still under debate (Kelley & Schwartz 2012). Kelley and Schwartz (2012) however, endorse age at first molar eruption as having a strong association with life-history. This study estimates M1 eruption in several *P.* and *Australopithecus* individuals based on previous age at death estimations determined through histological analysis (Kelley & Schwartz 2012). It was found that these age of eruption predictions were significantly younger than those made using either brain size or extant ape comparative models (Kelley & Schwartz 2012). These result were interpreted to mean one of three things: life-histories of hominins were faster than observed in all extant great apes, the presence of rapid early development and early weaning with an otherwise extended life-history fitting better with brain size estimations, or ages at death, on whole, had been underestimated (Kelley & Schwartz 2012).

When operationalising the application of an 'extant ape pattern', researchers often apply a chimpanzee odontogenetic model (as seen in Zuckerman 1928; Mann 2975; among others). As previously discussed, odontogenetic and life-history patterns are not consistent across all great ape species and likely the chimpanzee model is applied most often simply because it is the most well understood (due to thorough studies such as Nissen & Riesen 1964, Smith et al. 1994, and Hill et al. 2001). While it has been shown that early hominins did not display developmental patterns reflective of either extant apes or modern humans, as discussed above, this hypothesis presents a further issue. By stating early hominin developmental patterns were likely intermediate between extant apes and modern humans, it would seem logical then to estimate a modern human age, estimate an extant ape (or chimpanzee) age, and assign the fossil individual an age at death that is exactly intermediate.

This is problematic on multiple fronts. Firstly, very little is known about the behavioural patterns of early hominins. As it has been demonstrated that behavioural responses to unique adaptive pressures can influence odontogeny (Bronikowski et al. 2011; Schwartz 2012), this lack of knowledge hinders researchers' ability to interpret hominin developmental patterns. Secondly, as is the problem with a homogenous great ape developmental model, it cannot be assumed that all early hominins developed the same way and exhibited equivalent life-history patterns. Thirdly, as will be demonstrated and discussed in detail in Chapter 3, differences within specific aspects of odontogeny, such as the delay between eruption of neighbouring dental elements, prevents the confident attribution of an extant age even for comparative purposes.

2.2.3.2 Histological Interpretation

As a growing number of studies presented flaws in the use of comparative methods for the interpretation of extinct taxa, research focus shifted increasingly towards histological studies. The assertion of multiple patterns of life-history change (Smith 1992), the impact of adaptively strategic behaviours (Bronikowski et al. 2010; Schwartz 2012), individual element function (Reid et al. 1998, Dean & Vesey 2008), extinct taxa exhibiting patterns that suit both modern human and gorilla (Bromage 1987; Aiello et al. 1991), as well as other previously discussed conclusions along these lines, have changed the way early hominin development and life-history can be approached. It has been firmly shown that the application of extant analogues with the intention of identifying an equivalent pattern is erroneous. Histology-based methodologies, however, limit the necessity of analogues and instead rely primarily on the individual under assessment. Additionally, this removes the need to speculate environmental and dietary pressures and the influence that may have been had on the developmental patterns of these species at a point in time. Instead, conclusions regarding development and life-history can be used to interpret these pressures.

Synthesising previous work, Smith (1991) examined three lines of evidence for the evolution of the modern human life-history: comparative studies, chronological age, and developmental sequences. The first was, until recently, the most common method applied to this question. Comparative great ape analogues require a strong correlation between certain variables such as brain and body size with developmental milestones, to be at all useful (Smith 1991). This method estimated australopith species would have a short, chimpanzee-like lifespan and an M1 erupting between 3 and 3.5 years of age based on the small body and brain of this hominin (Smith 1991). The second analytical technique involves measurement of incremental growth lines displaying enamel deposition to determine an absolute chronological age (Smith 1991). Smith (1991) applied this method to three australopith specimens and determined an M1 eruption age of approximately 3.25yr. The third technique often operates on a coefficient of variation of human dental age. This method indicated that *Australopithecus* and extant apes both diverge significantly from modern humans (Smith 1991). The combination of these three lines of

evidence led to the conclusion that the rate and pattern of life-history seen in modern humans was absent in australopith species and likely began to develop after the appearance of the genus *Homo* (Smith 1991). The reliability of comparative analogues for accurate age at death determination as compared to histological interpretations is discussed and assessed further in Chapter 3.

With the information available to them at the time, Bromage and Dean (1985) re-examined age at death attributions for immature fossil hominins. This study asserted maturation and life-history of hominins was more similar to great apes rather than modern human (Bromage & Dean 1985). As such, Bromage and Dean (1985) criticized previous age attributions as these ages were based on modern human maturation, dental development, and dental wear models. To avoid the pitfalls of applying a purely analogous model, Bromage and Dean (1985) conducted a study into incremental growth striations in enamel. Using this method, the study aimed to attribute species-specific ages at death in order to interpret the palaeodemography and growth patterns of early hominins (Bromage & Dean 1985).

A sample of *Australopithecus afarensis*, *Australopithecus africanus*, *P. robustus*, and early *Homo* (1, 1, 4, and 2 individuals, respectively) was assessed (Bromage & Dean 1985). The latter category was represented by a *Homo erectus sensu lato* specimen from East Turkana in east Africa and an indeterminate "Early Homo" specimen from Swartkrans, South Africa (Bromage & Dean 1985). It was determined that these hominins had an enamel deposition periodicity of 7-8 days, as opposed to the 4-8 days in modern humans (Bromage & Dean 1985). However, there are multiple issues with this conclusion. Specifically, the small sample size, combining four species to create one population without taking temporal or regional variation into account, and the apparent complete overlap of with modern human periodicities. A further variable is the estimations and assumptions required for this study. In modern humans, enamel is forming for approximately six months before the striae become visible in the location observed in this study (Bromage & Dean 1985). Though it is hypothesised that this time period may be smaller in great apes, the modern human time was used for this estimation

as well as for the estimation of the period between birth and the onset of calcification (3 months; Bromage & Dean 1985).

With these assumptions in mind, Bromage and Dean (1985) allowed that the crown formation times yielded by this study are likely more reliable than the age at death estimations. It was concluded, nonetheless, that the calculated ages of these four species are equivalent to approximately two thirds that of modern humans (Bromage & Dean 1985). It was also observed that the period of root extension was significantly shorter in these early hominins than in modern humans (Bromage & Dean 1985). These early studies began to acknowledge the problems in comparative analogues and so supplemented studies with histological methodologies. However, research had not yet broken free of the paradigm calling for the placement of early hominins into either a great ape category or a modern human category. Conclusions such as formation and root extension periods do not require additional comparative information and are determined solely on histological data and so are more reliable. Once the interpretation begins to include conclusions aligning extant hominins with either great apes or modern humans however, many of these studies must be discounted due to more recent research.

Dividing the dental arcade into posterior (postcanine) and anterior (incisal) dentition for the purposes of assessment is one of the first steps made towards breaking this problematic paradigm. Beynon and Wood (1987) studied a sample of East African 'robust australopiths' (*P.*) and early *Homo* for the purposes of determining patterns and rates of enamel growth in posterior teeth. Previous studies claimed that the incisors of these species formed more rapidly than those of modern human. Beynon and Wood (1987) criticized previous work on the basis that these studies examined surface manifestations of enamel formation and so were less accurate and that assumptions made—enamel increments in hominins being similar to modern humans, for example— weakened these studies.

Beynon and Wood (1987) instead studied fractured molar teeth, examining both long- and short-period incremental growth markers within the enamel. Results indicated crown

formation times in posterior teeth were shorter than those recorded for modern humans (Beynon & Wood 1987). This pattern was even more evident in the particularly thick-enameled molars of the *P.* (Beynon & Wood 1987). It was also concluded that hominin dentition erupted more rapidly than that of modern humans (Beynon & Wood 1987). As this pattern appeared to correlate with enamel thickness, it is possible to link these finds back to element functionality (Reid et al. 1998).

Critical of previous attempts to attribute age at death to fossil specimens based on extant analogues, both human and ape, Beynon and Dean (1988) conducted a purely histological study using incremental growth lines to create a timescale specific to the extinct species rather than to support or oppose different analogical models. Using a sample of *Australopithecus* and *P.* mandibles, Beynon and Dean (1988) determined that not only was early hominin odontogenesis different from both modern humans and extant apes, but these two genera differed from each other in both crown formation times and developmental sequence. Consistently however, all early hominin specimens examined exhibited shorter periods of dental development than modern human, interpreted here as shorter childhood periods (Beynon & Dean 1988). While it was asserted that broad patterns such as a relatively shorter developmental period applies to both *Australopithecus* and *P.*, the critical conclusion drawn from this study is the distinction between the two. Many earlier studies, discussed previously, assessed the australopiths under the assumption that equivalent developmental and life-history patterns would apply to both genera.

Early in the history of hominin odontogenetic studies, Broom and Robinson (1951) asserted that while *Australopithecus africanus* closely resembled extant apes in dental eruption pattern, *P. robustus* instead resembled modern humans. Grine (1987) called into question previous studies (Dean 1985) supporting this theory. Grine (1987) examined the *P. robustus* specimens used in this earlier study from both Swartkrans and Kromdraai B (SK 61, SK 62, SK 63, and TM 1536). It was found that in this species, permanent incisors are advanced both in formation and eruption stages as compared to the first permanent molars (Grine 1987). While Grine (1987) accepted the conclusion that

Australopithecus africanus dental patterns closely resembled those of great apes, he asserted that the observed pattern in *P. robustus* did not hold constant across the species. Instead, Grine (1987) pointed to faults in observation, specifically the misidentification of deciduous incisors in SK 61 as permanent dentition. The other three specimens were concluded to exhibit ambiguous and non-distinct patterns leading Grine (1987) to dismiss theories drawn from Broom and Robinson's (1951) study.

Aside from Grine (1987) still accepting the attribution of an extant pattern to an extinct species, it is important to note that often due to technological shortcomings, many early studies such as Broom and Robinson (1951) contain misinformation that, upon reassessment, can be refuted. Additionally, while it may seem problematic to see non-distinct patterns within these individuals, it actually speaks to an important point. A portion of this will be due to the need for specimens to be reconstructed (Grine 1987) and small sample sizes within palaeo-populations. The non-descript nature of these individuals, however, may be indicative of a species exhibiting an adaptive strategy not seen in either extant model. If odontogeny maps onto behavioural and functional adaptations to specific adaptive strategies (Reid et al. 1998; Dean & Vesey 2008; Bronikowski et al. 2010; Schwartz 2012), the failure of the observed *P.* pattern to adhere to either model would suggest a different suite of these variables in *P. robustus*.

As commentary to Mann's (1975; discussed in depth in Chapter 3) early work concluding dental development patterns of hominins were similar to modern humans—indeed, similar enough to use modern human odontogenetic models for direct age interpretation—Smith (1986) assessed dental development patterns in *Australopithecus* and early *Homo*. Smith (1986) aimed to interrogate Mann's (1975) hypothesis that extended maturation seen in modern humans occurred very early in the hominin lineage and included these genera.

Smith's (1986) sample included specimens representing *Australopithecus afarensis, Australopithecus africanus, P. boisei, P. robustus, Homo habilis*, and *Homo erectus* (as represented by ER 820 and 1507). This study examined incremental growth lines in tooth

enamel for each of these species. In direct contrast to Mann's (1975) study, Smith (1986) reported short developmental periods for all included species. These results suggested early hominin resemblance to great apes as opposed to modern humans even as recently as *Homo erectus* (Smith 1986). Despite still referring to the binary states of ape-like or modern human-like, the conclusion that hominins developed significantly faster than modern humans, inclusive even of *Homo erectus*, is notable. While such comparative analogues are ineffective, conclusions such as these contribute to the determination of the evolutionary trajectory of the modern human life-history patterns.

While many studies of internal microstructure focus on molar teeth, Dean and Reid (2001) examine perikymata spacing and distribution on the anterior teeth of hominins in reference to extant populations of modern humans and extant great apes. A study such as this is particularly significant due to the debate concerning the anterior versus posterior dental development in *P.* (Beynon & Wood 1987). Five *Australopithecus afarensis* teeth, 22 *Australopithecus africanus* teeth, six *P. boisei* teeth, 27 *P. robustus* teeth, 115 modern human teeth, and 30 extant African great ape teeth were examined along the buccal face of the crown in ten height divisions (Dean & Reid 2001).

Crown formation times were calculated by summing lateral and cuspal formation times determined from perikymata counts combined with known and presumed periodicities (Dean & Reid 2001). A clear distinction between the hominin sample and the extant great apes was evident (Dean & Reid 2001). Crown formation results in the australopiths were significantly shorter than both modern humans and great apes (Dean & Reid 2001). Internal microstructure such as perikymata spacing was found to lack a clear distinction between *Australopithecus* and *P.* despite showing differences in mean value (Dean & Reid 2001). Contrary to previous studies (Bromage 1987; Aiello et al. 1991), assessment of the internal microstructure of *P.* molars showed no similarities to those belonging to the gorilla (Dean & Reid 2001). It was also hypothesised that significant differences would be seen within the dental microstructure of the genus *Homo*, particularly between *Homo ergaster,* and *Homo rudolfensis* and *Homo habilis sensu stricto* (Dean & Reid 2001).

Many of these previous histological studies of early hominins did little, if anything, to differentiate between the species included in the sample and instead examined specimens by genus or grade (i.e. australopith). Even some of the studies that sampled a variety of species, often presented broader conclusions. Lacruz et al. (2006) examined variation in enamel development across fossil hominins in South Africa. Using portable confocal microscopy, a large sample of *Australopithecus africanus* and *P. robustus* was studied to determine cross-striation periodicity of enamel deposition specific for each species (Lacruz et al. 2006).

It was found that there was a mean periodicity of seven days for both species, however, there was evidence for the presence of different mechanisms of amelogenesis and, so, dental development (Lacruz et al. 2006). In *P. robustus*, ameloblasts show high rates of differentiation throughout the cervical enamel, and the lateral enamel seems to form much more quickly than the cuspal enamel (Lacruz et al. 2006). In *Australopithecus africanus*, these two factors are just the opposite (Lacruz et al. 2006). In addition, there appear to be fewer lateral striae of Retzius in *P. robustus* than in *Australopithecus africanus* (Lacruz et al. 2006). These developmental patterns allow both of these species to maintain a much shorter dental formation period than modern human despite larger crown size and thicker enamel (Lacruz et al. 2006). This is a clear example of a functional adjustment made to allow for a particular adaptive strategy manifesting in odontogeny.

With aims to continue species distinctions in dental microstructure studies, Lacruz et al. (2008) examined the role of megadontia, as defined by the megadontic quotient (McHenry 1984, 1988), in striae periodicity and enamel secretion patterns in early hominins. It was previously established that despite large crown size and thick enamel, dental developmental periods in early hominins were much shorter than that of modern humans (Dean & Reid 2001; Lacruz et al. 2006). This is due to a much quicker rate of enamel deposition in these thick-enamelled hominins (Lacruz et al. 2006). To gain a more comprehensive understanding of this process, Lacruz et al. (2008) recorded enamel

deposition striae of seven different species (*Australopithecus anamensis, Australopithecus afarensis, P. aethiopicus, P. boisei, Homo rudolfensis, Homo habilis,* and *Homo erectus*) represented by 17 molar teeth. Daily growth increments were compared to the megadontic index of each species to assess the relationship between growth rates and tooth size (Lacruz et al. 2008).

It was found that a considerable amount of variability existed across the species sampled (Lacruz et al. 2008). Contrary to Lacruz et al. (2006), all species appeared to conform to the pattern of a higher number of striae in the outer rather than the inner enamel and the cuspal rather than the cervical (Lacruz et al. 2008). It was found that the higher the megadontic quotient, the faster the enamel formed (Lacruz et al. 2008). This phenomenon would explain how large-toothed hominins developed their dentition in a shorter time than small-toothed hominins. It was also suggested that frequency of long-period striae expressed a strong correlation with male and female body mass (Lacruz et al. 2008). Lacruz et al. (2008) suggested a potential for taxonomic distinctions based on these results despite the variability of long-period line periodicity of these species falling within the range of modern humans. It appears the rate of deposition accelerates to accommodate for thicker enamel and so results in developmental times that can reflect phylogenetically and adaptively disparate species.

Dean and Lucus (2009) discussed dental as well as skeletal growth in early hominins. Many studies in this time period had moved away from attempting to correlate odontogeny to skeletal growth markers. Dean and Lucus (2009) examined this potential correlation in terms of 'proportions of life', in a similar fashion to Smith's (1992) 'scale of life' theory. Dean and Lucus (2009) were also very critical of using modern human comparisons be it a direct analogue or used in conjunction with another methodology as, by this point, it was generally agreed that early hominin odontogenesis did not reflect that of modern humans. Interpretations based on the microstructure of enamel and dentine however, consistently predict ages significantly younger than those provided by modern human radiographic comparisons (Dean & Lucus 2009). In fact, comparative evidence suggests an acceleration in growth early in life resulting in a greater proportion of final

adult body mass and stature being achieved much earlier in these early hominins (Dean & Lucus 2009). Dean and Lucus (2009) assert the hypothesis that early hominins, such as the australopiths, grew most similarly to apes, though more recent hominins, such as *Homo erectus*, exhibited a prolonged, if not completely modern human-like, growth period. It must be noted that while 'ape-like' and 'modern human-like' were still commonplace terminology, they were no longer considered the only options in a binary system. That is, 'ape-like' implies faster paced odontogeny and a more rapid life-history, while 'modern human-like' implies slower odontogeny and a more prolonged life-history.

Smith et al. (2015) criticises all studies using modern human or great ape comparative analogues, calling them circular and blaming them for creating the false binary state of ape-like or modern human-like. Instead, Smith et al. (2015) use X-ray synchrotron imaging to virtually study the dental microstructure of over 20 hominin specimens (including *Australopithecus anamensis, Australopithecus africanus, P. robustus,* and South African early *Homo*) for the purposes of determining an exact chronological age at death and assess dental development. First molars at a specific stage of development (crown formation complete, unerupted; older individuals who did not fit this criterion were aged by finding matching striation in a neighbouring tooth) for this study and long-period lines were used to determine chronological age (Smith et al. 2015). The M1 was selected because this element preserves a neonatal line and so can be aged absolutely; specimens in which this line could not be found were assumed to have begun formation at birth (Smith et al. 2015).

As periodicities were found to range from 6-12 days consistently across the sample, no evidence was found to support the hypothesis that australopith species have lower mean values than observed in all *Homo* species, fossil or extant (Smith et al. 2015). Both australopith and early *Homo* samples show crown formation times that overlap or fall just below that of modern humans, while the *P.* sample showed significantly shorter formation times (Smith et al. 2015). The results of this study were highly variable and it

is argued that previous studies using less rigorous techniques are likely to be in error (Smith et al. 2015).

Histological as opposed to comparative methodologies have improved both the resolution and the reliability of conclusions drawn from extinct life-history studies. Many of these improvements come from the limited reliance on extant comparative data. While assumptions are still made based on extant species, interpretations are no longer based solely on these models. However, these interpretations are still hindered by previous methodologies. Even conclusions drawn from histological studies independent, or relatively independent, from comparative data are discussed in terms of extant species. To an extent, this can be useful. Insofar as life-history and development patterns are reflective of adaptive strategy, assessing extinct results through the lens of species with known adaptive strategies can be informative. However, situations such as that evident in *P. robustus* (anterior dentition more similar to modern human, molar dentition more similar to gorilla) are likely indicative of an adaptive strategy not exhibited in any living primate. Further functional analysis may elucidate the implication of such a 'mosaic' of developmental and life-history characteristics.

Despite these shortcomings, histological methodologies can avoid issues of error due to temporal and geographic range. Even comparative studies that did not discuss australopiths, for example, as a taxonomically and developmentally uniform group, suffered from these problems. A comparative sample selected from a single genus or even a single species could still potentially consist of individuals separated by nearly 1 million years (3.03-2.01 Ma; Pickering & Kramers 2010; Herries & Shaw 2011; Herries et al. 2013). As it cannot be logically assumed that individuals even within the same species would have been under identical environmental pressures and adhered to identical adaptive strategies, it cannot be confidently asserted that these individuals would have exhibited identical life-history and developmental patterns. As such, when included within a comparative sample, the results will likely be erroneous and display an inaccurately large range of variation. Histological studies avoid this issue by determining dental development patterns of individuals independently.

2.2.4 *P. robustus*

As discussed in Chapter 1, this study focuses on *P. robustus* and, more specifically, a *P. robustus* sample that has been identified to potentially represent a palaeo-population. As with all hominin species, life-history and developmental interpretations of *P. robustus* have a varied past. Often early studies did not differentiate between australopith species, obscuring specific interpretation. Studies have aligned *P. robustus* with either a great ape developmental model (Smith 1986) or a modern human developmental model (Broom & Robinson 1951; Mann 1975; Conroy & Vannier 1991a). It has also been proposed that while the incisors of this species align with a modern human developmental pattern, the molars are most similar to the gorilla (Bromage 1987; Grine 1987; Conroy 1988). This latter hypothesis is more useful in that it is the first to imply that extant analogues cannot be applied to *P. robustus*, or any hominin species. Odontogenetic models utilise each dental element to determine the age of an individual based on the composite developmental stages. As the anterior and posterior portions of the same individual cannot be made to adhere to a single analogue, it becomes clear that analogues cannot be accurately applied. Variance in support of one analogue versus another are grounded in a researcher's decision that the specimen in question fits one model sufficiently.

As *P. robustus* is accepted as a sister taxon and not included in the lineage ancestral to modern humans, similarities between the developmental patterns of these two species were not anticipated (Bromage 1987). It was proposed that the development of the anterior dentition of *P. robustus* resembled modern human only superficially (Bromage 1987). It has been shown that while the incisor development of this species may resemble that of modern human, molar development occurs over a notably shorter period (Lacruz et al. 2006; Smith et al. 2015). High rates of ameloblast differentiation have been found to allow the megadontic molar teeth of *P. robustus* to form rapidly despite thicker enamel and larger crown size (Lacruz et al. 2006).

It is possible, however, that this pattern supports the hypothesis of differential element importance (Dean & Vesey 2008). This trend of increasingly rapid enamel deposition

across megadontic species (Lacruz et al. 2008) suggests a functional adaptation to accommodate time necessary to develop dentition with thick enamel within a more rapid life-history. That is, the rapid development of molar teeth despite extremely thick enamel versus a relatively slow development of incisal teeth, may indicate a higher importance of the former within the *P. robustus* adaptive strategy. While *Homo* and *Au. africanus* incisors appear to have a slicing function, *P. robustus* incisors appear to have a crushing or grinding function as they occlude apically as opposed to occluding centrically. If this is the case, it indicates that the ability to crush and grind food directly following weaning is crucial to the *P. robustus* adaptive strategy. It would therefore be reasonable to assume the molar teeth would be of higher importance in this species.

In regards to an identified eruption pattern specific to *P. robustus*, conclusions are limited. Broom and Robinson (1951) suggested the relationship between M1 and I1 eruption was synapomorphic between *P. robustus* and modern humans with these elements forming and erupting simultaneously. Following studies such as Dean's (1987) supported this hypothesis stating that unlike other hominins, crown formation correlates closely between these two elements. However, Conroy (1988) asserted that the apparent disparity in molar versus incisor development pattern in *P. robustus*, as discussed, makes this hypothesis unlikely. Identification of a species-standard odontogenetic pattern may continue to prove difficult, however, as it has been asserted that observed patterns are not consistent across *P. robustus* and age determination is often ambiguous (Grine 1987). Histological studies have shown high variation as well as significant overlap between species (Smith et al. 2015). It is possible, though, that this is an artefact of sample heavily biased by time averaging. If this is the case, the study of palaeo-populations, or more constrained samples, may work towards resolving some of these issues.

3. Mann and Palaeodemography

As discussed in Chapter 2, Mann (1975) conducted a palaeodemographic study of the fossil hominin assemblages at the palaeo sites of Taung, the Makapansgat Limeworks, Sterkfontein Member 4 (or Type Site) and Member 5 decalcification (West Pit-Extension Site; see Sterkfontein context discussion above), Swartkrans Member 1, and Kromdraai B Member 3 (Figure 1). His study addressed the palaeodemography of *Australopithecus africanus, P. (Australopithecus) robustus,* and early *Homo* sp. (sometimes referred to in his study as *Homo erectus* or *Telanthropus*; Mann 1975). As the focus of this study is *P. robustus*, only the section of Mann's (1975) study related to this species has been addressed. Consequently, work conducted on material from Taung, the Makapansgat Limeworks, and Sterkfontein will not be included. It should be noted that some researchers have attributed certain Sterkfontein hominins from Member 5B to *P. (Australopithecus) robustus* (Kuman & Clarke 2000; Herries & Shaw 2011) however, as this has been disputed intermittently and would result in an insignificant sample size in any case, these specimens have been excluded from this study. Additionally, a small number of species attributions suggested by Mann (1975) have since been either disproven or are disputed, resulting in the inclusion of specimens no longer considered to belong to *P. robustus,* and exclusion of specimens now attributed to this same species. As it was not possible to access the original fossil material for the purposes of confirming species designations, this study proceeds as per the species attributions in Mann (1975).

3.1 The Mann Method

Mann's (1975) study aimed to determine the minimum number of individuals (MNI) for hominins within each assemblage and establish an age at death profile for these specimens. The results of these analyses were then used to ascertain the palaeodemography of the populations represented in these assemblages. Despite a number of methodological failings that will be elucidated below, Mann's (1975) study represents the most thorough evaluation of South African hominin MNI, age at death, and palaeodemography to date, and so is the necessary starting point for the evaluation of the Drimolen *P. robustus* material.

3.1.1 MNI Determination

Mann (1975) separated MNI determinations into three categories:

- Those accepted in published literature as one individual; those that physically join together exactly to form a complete piece
- Those with an "excellent chance of belonging to the same individual"
- Those with "a reasonable chance of belonging together"; (Mann 1975, p.12-13)

Categorisation was based on the strength of agreement in the four set criteria of size, age, wear, and cusp pattern (Mann 1975). These criteria were assessed by comparing a range of variables including stage of development, stage of wear, interproximal faceting, occlusal faceting, and preservation and staining. For the purposes of this study, all three of Mann's (1975) categories were interpreted to represent the most conservative possible MNI (Figure 5). This was done to ensure MNI data taken from Mann's (1975) study could be accurately compared to the Drimolen MNI data, as the latter represents a conservative conclusion. Problematically, MNI attributions, as well as certain species attributions, have been re-evaluated and specimen descriptions appear inconsistent between the Mann (1975) publication, subsequent publications (Brain 1981; 1993), the Ditsong electronic catalogues, and direct visual assessment conducted by this author. These inconsistencies reduce confidence in Mann's (1975) conclusions as well as in conclusions drawn from comparisons between Mann's data and the Drimolen data.

CATALOG NUMBER SK-

1	2 SAME AS 4	3 SAME AS 4	4 SAME AS 8	5	6	7	8 SAME AS 7	10	11	12	13	14 SAME AS 13	15	16	17
18 SAME AS 13	15(b) PC	19	20	21	2(a) SAME AS 21	22	23	24	25	26	27	28	29 T	30	31
32	33 SAME AS 26	34	35	36	37	38 T	39	40 T	41 SAME AS 34	42	43	44	45	46	47
48	49	50 PC	52	54 C	55	56(b) SAME AS 55	57	61	62	63	64	66	65(a) SAME AS 66	66	67 SAME AS 65
68 T	69 T	70 T	71 T	72	73 SAME AS 69	74(a)	74(b) T	74(c) SAME AS 65	75	79	80 SAME AS 43	81	82 PC	83	84 PC
85 PC	85(a) SAME AS 93	86 T	87 T	88	89	90 SAME AS 89	91 SAME AS 89	92 T	93 T	94 T	95 SAME AS 48	96	97 PC	98	99 SAME AS 47
100 SAME AS 6	101	102	104 SAME AS 62	105 SAME AS 99	438	821	822	823	824	825	826(a)	826(a) LM^2	826(b)	827	828 SAME AS 1
829	830	831	831(a)	832	833	834	835	836	837	838(a)	838(b) SAME AS 102	839	840	841(a)	841(b)
842	843 SAME AS 75	844	845	846(a) SAME AS 843	846(b) SAME AS 847	847 SAME AS 80	848 SAME AS 847	849	850 SAME AS 72	851	852	853 PC	854 PC	855 SAME AS 840	856
857	858 C	859 C	860 PC	861	862	863	864	865	866	867	868	869	870	871	872

873 T	874	875	876	877 SAME AS 826(a)	878	879	880 SAME AS 22	881	882 SAME AS 881	883	884 T	885	1312	1314	1524
1565	1566	1567	1568	1589	1590	1591 SAME AS 17	1592	1593	1594	1595	1596	1648	1649	3155(b) PC	3974
3975	3976	3977	3978	3981(a) PC	3981(b) SAME AS 3981(a)	14000	14001	14003	CATALOG NUMBER SKW-						5(a)
5(b) SAME AS 5(a)	6	7 SAME AS SK43	8(a)	8(b)	10	11	12	14	15	27 PC	29	30	31 SAME AS SK 877	32	33 SAME AS SK 886(a)

MINIMUM NUMBER OF INDIVIDUALS POSSIBLE: 27   MAXIMUM NUMBER OF INDIVIDUALS POSSIBLE: 218

LEGEND   218

▨	FOSSILS THAT BELONG TO THE INDICATED INDIVIDUAL	-14
▥	EXCELLENT CHANCE THAT FOSSIL BELONGS TO THE INDICATED INDIVIDUAL	-8
▤	REASONABLE CHANCE THAT FOSSIL BELONGS TO THE INDICATED INDIVIDUAL	-19
C	SMALL CRANIAL PIECES ASSUMED TO BELONG TO ONE OR ANOTHER MAJOR CRANIAL FOSSIL	-2
PC	POSTCRANIAL BONES ASSUMED TO BELONG TO ONE OR ANOTHER MAJOR CRANIAL PIECE	-12
T	ANTERIOR TEETH ASSUMED TO BELONG TO ONE OR ANOTHER MAJOR CRANIAL PIECE	-15
		148

Figure 5: Swartkrans MNI from Mann (1975)

70

3.1.2 Age at Death Determination

3.1.2.1 Interpretive Model

Prior to Mann's (1975) work, the chronological age at death of fossil hominins was interpreted predominantly through the application of either a great ape or modern human odontogenetic pattern. Clark (1967) asserted that wear patterns evident on the permanent molars of australopiths more closely paralleled the pattern as seen in modern human. Following this argument and his own assessment, Mann (1975) modelled age interpretation on the modern human pattern, as per Kronfield (1954). In the absence of an express methodological explanation, it must be assumed that Mann (1975) proceeded on the assumption that the delay between molar eruption-succession is clearly reflected in degrees of occlusal and interproximal wear. This inference can be supported on the basis that all wear studies operate under this assumption (such as Massler & Schour 1946; Miles 1963).

Mann's (1975) study used the standard stages of dental formation suggested by Garn and Lewis (1963):

1. Stage of the follicle
2. Beginning calcification of the cusps
3. Crown completion and beginning of root formation
4. Alveolar eruption
5. Gingival eruption
6. Attainment of the occlusal level
7. Apical closure

These stages were utilised both in his assessment of the great ape versus modern human models, and later in his age at death determinations of the hominin assemblages. Mann (1975) took into account dental patterns for chimpanzees as well as modern humans, as *Pan troglodytes* represents the closest phylogenetic relative of modern *Homo sapiens*.

His investigation into previous studies yielded varied results in regards to the relationship between chimpanzee and modern human dental development patterns (Zuckerman 1928;

Schultz 1935; Nissen & Riesen 1945). The variance in these hypotheses at the time of Mann's (1975) study led him to set the clarification of dental development patterns as one of his aims. Using x-rays of three juvenile and sub-adult *P. robustus* fossils (SK 64, SK 63, and SK 843) in comparison to modern human and chimpanzee models, Mann (1975) determined australopiths followed a dental development pattern of modern human populations.

Until the late 1900's and into the early 2000's, it was commonly thought that developmental patterns of early hominins would resemble either that of modern *Homo sapiens* or that of extant apes, becoming progressively more *sapiens*-like through the *Homo* lineage (Bromage & Dean 1985; Beynon & Dean 1988; Smith & Boesch 2011). However, as discussed previously, the concept of a "great ape model" is illusory, as the members of this group do not hold to a homogenous developmental pattern. It is now known, for example, that the timing of chimpanzee dental development moves approximately half as quickly as that of modern human (Nissen & Riesen 1964) and life-history stages of the gorilla are proportioned in an entirely unique pattern (Aiello et al. 1991; Macho 2001).

The literature debating the merits of applying a modern human or an extant ape model is copious (Zuckerman 1928; Schultz 1935; Nissen & Riesen 1945; Simpson et al. 1990; Smith 1991). The aforementioned studies were based primarily in qualitative comparisons between fossil material and often biased, extant population samples. Demographics and age profiles were consequently modelled on whichever analogue was considered the best fit by the researcher. Even disregarding the fact that the gorilla (*Gorilla gorilla)*, the chimpanzee (*Pan troglodytes* and *Pan paniscus)*, and the orangutan (*Pongo pygmaeus* and *Pongo abelii)* do not hold to a homogenous "great ape model", this disagreement created a problem with consistency and limited the ability to compare data sets. As described above, Mann (1975) personally assessed these two analogues and concluded australopiths closely resembled modern humans.

In more recent years, a consensus has emerged among researchers that the odontogenetic profile of our early human ancestors reflects neither a chimpanzee profile (commonly used due to the species' close phylogenetic relationship with *H. sapiens*) nor the modern human profile, and instead sits in between (see discussion in Chapter 3). The danger with this hypothesis lies in the tendency to estimate an age at death simply by determining an equivalent chimpanzee age and an equivalent modern human age, and assigning a median age to the fossil individual. Assigning specific chronological ages at death in this manner is based on the assumption that dental development has moved from 'primitive' to 'derived' consistently, linearly, and non–logarithmically. This is an assumption that has no grounding and is unlikely to be true across multiple other morphological features. This situation becomes doubly problematic when applied to *P. robustus* and other species thought to belong to a sister taxon to the *H. sapiens* lineage, as these assumptions would be unlikely to hold in this circumstance even if it was true within a direct ancestral lineage. For this reason, age assignment and odontogenetic interpretation cannot be confidently determined using either a great ape or a modern human analogy.

3.1.2.2 Fossil Hominin Interpretation

At the time of Mann's (1975) study, however, researchers were divided on the question of whether extinct hominins adhered to a modern human or great ape odontogenetic model (see discussion above). After his own assessment of three juvenile *P. robustus* specimens, Mann (1975) came to the conclusion that these species followed a modern human developmental pattern. Due to this, Mann's (1975) age at death determinations were interpreted from a modern human dental development, eruption and wear model based on Miles' (1963) technique of functional age and Massler and Schour's (1946) formation and eruption standards.

Miles (1963) assessed methodologies used at that time for attributing age to fossil materials. He mentioned approaches such as examination of epiphyseal fusion and early dental development stages (for example, those outlined in Massler and Schour's [1946] work) as reliable techniques for aging young individuals to an accuracy of a few weeks

(Miles, 1963). In his study, Miles (1963) worked to extend the accuracy of age determination beyond this limited bracket.

Using a study put forward by Massler and Schour (1946) that had determined dentine of deciduous teeth was deposited at a rate of approximately 4µ per day, Miles (1963) counted the longitudinal sections between the neonate line and the enamel deposited until death on a sample of Anglo-Saxon remains. Miles then compared striations within multiple dental elements within an individual to compensate for damage or interruption within a single tooth. Miles' study showed that, while it did not allow for a range of variation or sexual differences, the dental development charts presented by Massler & Schour (1941) worked as a usable tool for interpreting age at death for individuals below the age of 15 (Miles, 1963).

Miles (1963) critiqued previous work on methodologies and techniques for aging mature individuals. It was Miles' (1963) view that, for example, Gustafson and Malmo's (1950) work assigning a 0-3 point scale to characteristics such as cementum thickness, pulp cavity size, degree of wear, and state of supporting tissues to determine age, was based on a strong principle but unhelpful in practice. While Miles (1963) commented on the unreliability of a modern analogy of wear patterns for archaeological application due to variance in occlusal stress, this is the basis for his technique of functional age. The goal of developing this methodology was to accurately track rate of occlusal wear as it changed through life for the purposes of accurately aging adult individuals (Miles 1963).

Miles (1963) further examined a sample of 38 individuals of "known age" to assess the rate of wear on permanent dentition. In this study, he most closely documented wear patterns of molar teeth, noting that premolars wear nearly in parallel with molars, and incisor wear was too "erratic and variable" (Miles, 1963).

Miles categorized wear into broad stages: polishing of cusps, appearance of facets that then increased in number and size regularly, and appearance of small dentine exposures at the top of the cusps that then expanded in size (Miles, 1963). He noted little variation

within the sample and interpreted this as lack of significant individual variation, although this may be a product of the constraints of the sample. He also noted the rate at which mesial facets (interproximal wear facets or flat, worn planes produced by adjacent teeth coming into contact with one another) appear between neighbouring teeth.

Miles took the rate of occlusal and interproximal wear and joined it with the previously discussed models of dental development. By tracking wear rates along a predictable timeline, he determined the "functional age" of the specific element; that is, the amount of time the individual tooth had been a "functional unit in the mouth" (Miles, 1963). This age was then added to the known ages of eruption for the chosen element, resulting in the age of the individual as a whole (Figure 6).
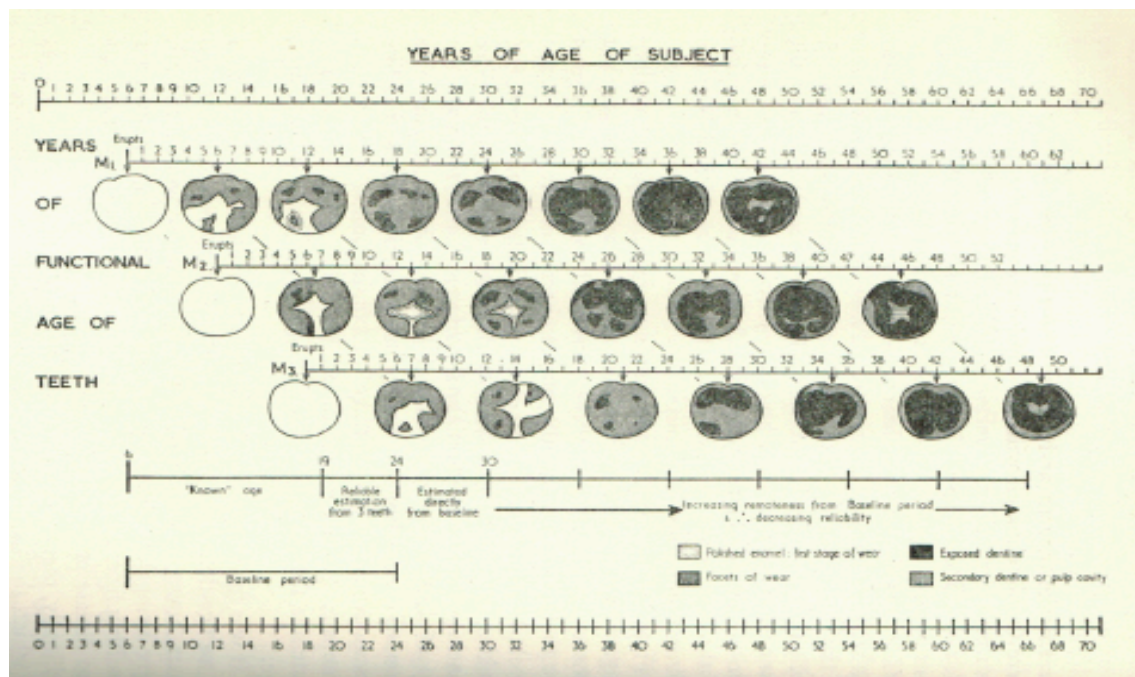
Figure 6: Functional Wear to Estimate Age; From Miles 1963

This was, of course, only assessed in terms of modern human populations from a specific area. Variables such as diet, nutrition, and pathology (many of the individuals examined died young due to terminal illnesses) jeopardize the integrity of this study even in reference to differing modern populations. Known difference between modern human

patterns and those of our early human ancestors preclude the application of this method to studies of fossil hominins almost entirely.

3.2 The Mann Method at Swartkrans and Kromdraai B

Problems exhibited in MNI determination are compounded when combined with Mann (1975) age attributions. The first issue arises directly from the MNI data. Subsequent studies have placed together specimens Mann (1975) had separate. The combining of these into one individual often creates a very large age range for the individual as Mann's (1975) age determinations had the specimens in disparate age categories. Multiple issues also exist in the age determinations themselves. Moreover, as discussed previously, assigning ages to fossil hominin specimens based on a modern human pattern of formation, eruption, and wear has been proven to be inaccurate (see discussion in Chapter 2).

Ages of older individuals cannot be based on formation and eruption as all the dentition is in occlusion. These specimens must instead be assigned ages at death based on wear stages. Clearly, this does not escape the issues of inaccurate extant analogues outlined above. Wear stage assessment is based primarily on one factor: the rate of wear. The rate of wear can be used to determine the length of time a particular dental element has been in functional occlusion. Mann (1975) applied Miles' (1963) pattern of functional age to the Swartkrans Member 1 and Kromdraai B Member 3 assemblages. The accuracy of this method is reliant on the multiple assumptions that follow from applying a modern human development profile. It is assumed by Mann (1975) that the rate of wear in these early hominins is consistent with that of modern humans. As the rate of wear is reflective of diet, enamel thickness, and masticatory biomechanics, this is almost definitely not the case (Curry 2002; Fung 2013). Additionally, Miles' (1963) functional age assessment technique then requires the length of attrition to be added to the age at which the element comes into occlusion: a pattern unknown to researchers, as discussed above. Finally, wear stages described by Mann (1975) are discussed in a manner unrelated to Miles' (1963) functional age charts (i.e. "wear 1+" versus "four years of functional wear").

3.2.1 Assessment of the Results of the Mann Method

For the purposes of the substantive study undertaken as part of this thesis, it was necessary to convert age at death data provided by Mann (1975) for the Swartkrans Member 1 and Kromdraai B Member 3 *P. robustus*. However, due to the complications outlined above, this was not possible. The lack of internal consistency within Mann's (1975) data set, in combination with the inability to obtain access to digital data for the purposes of conducting a first-hand assessment, made anything beyond a preliminary comparison impossible.

Despite this, an evaluation of Mann (1975) age at death attributions was made. As discussed in the previous chapter, Smith et al. (2015) presented a set of age at death attributions determined through histological methods. By analysing enamel microstructures via synchrotron imaging, Smith et al. (2015) was able to determine exact ages at death for a small sample of early hominin specimens. This provides the unique opportunity to evaluate the ages put forward by Mann (1975). As shown in Table 2, the age ranges presented in Mann (1975) do not overlap with the exact ages presented in Smith et al. (2015). In fact, quite a large error is exhibited: up to 3.88 years in *P. robustus* and 13.48 years in *Au. africanus*. However, this comparison is not robust due to a small overlapping sample size.

Modern Human Ages vs Histological Ages
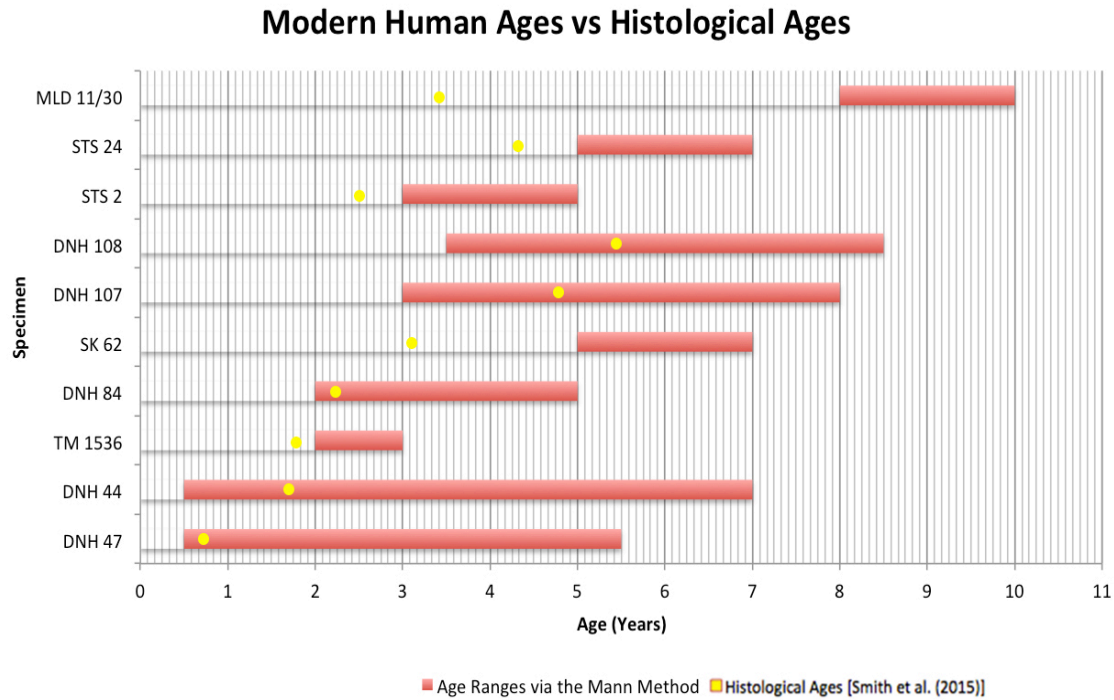
Table 2: Histological ages from Smith et al. (2015) versus ages determined through the "Mann Method"

3.3 The Mann Method at Drimolen

With that in mind, this author aimed to use the Mann (1975) age attributions combined with the discussion and reasoning of these attributions to create a comparable data set to the Drimolen assemblage. This sample data set was assessed using the "Mann Method" and used to evaluate the reliability of this technique for the possibility of calibrating the assigned human age to a species-appropriate age.

In regards to formation and eruption, two different modern human models were used. As in Mann (1975), the Massler and Schour (1946) developmental standards were applied. However, as this pattern differs marginally from patterns developed in subsequent years using larger and more varied sample sizes, a modern human model presented by Gustafson and Koch (1974) and Anderson et al. (1976) was also used. Predictably, as formation and eruption patterns of *P. robustus* clearly differ from that of *H. sapiens*, the use of these models resulted in internally contradictory aging data. For example, it wouldn't be unexpected to observe one element resembling an individual of 1±0.5 years

and another an individual of 6±1 years within the same specimen. As Mann (1975) assigned the most parsimonious age to the Swartkrans and Kromdraai B individuals, the attributions are often misleading and appear ill fit even within a modern human analogue. For the purposes of this comparative, an age range was presented.

While this expanded data set did show overlap between age ranges determined through the application of the Mann (1975) method and the exact ages presented in Smith et al. (2015), the error margins of the age ranges render this data nearly meaningless. Demographic and mortality profile studies require an age at death accuracy of ±2 months (Lyman 1994). The contradictory nature of dental elements within a single specimen yielded age ranges of, at most, 6.5 years (Table 4). Were this individual following an ontogenetic pattern of chimpanzee, this range would represent the difference between an infant and a sexually mature individual (Hill et al. 2001). Age ranges within the Mann (1975) data set, while in some instances spanning up to 10 years in the case of SK841b, most often sat between 1 and 6 years.
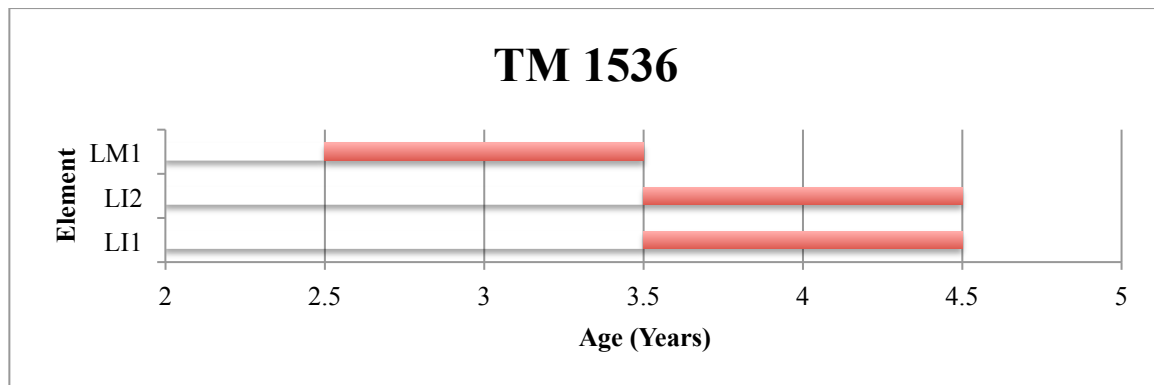
Table 3: Element-specific ages within TM 1536 interpreted based on a modern human model.
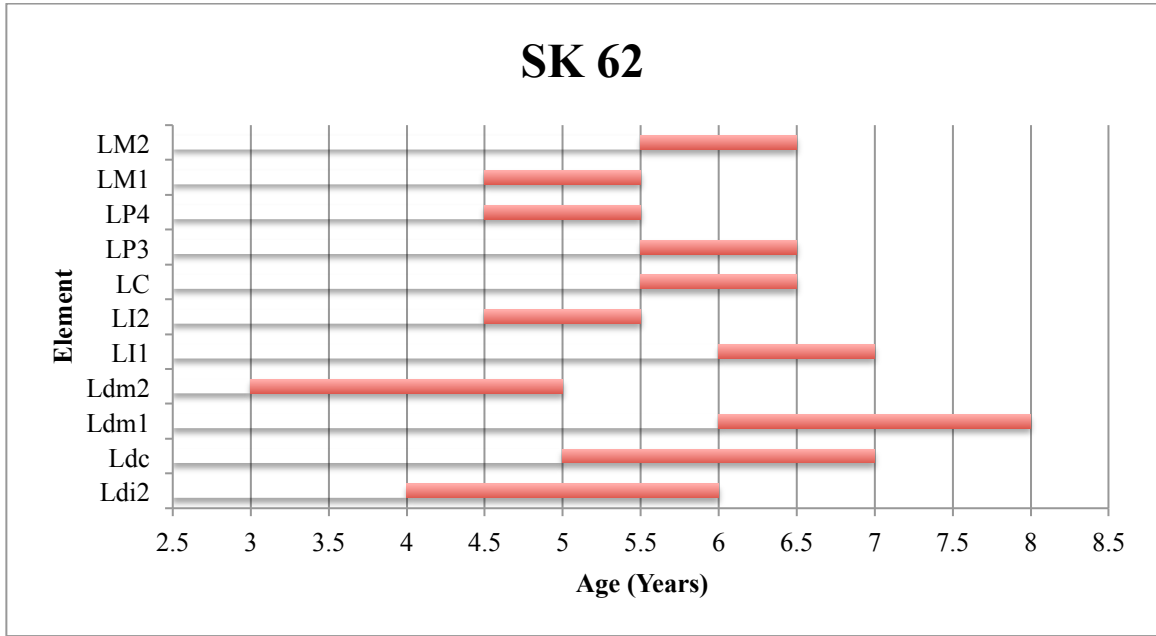
Table 4: Element-specific ages within SK 62 interpreted based on a modern human model.
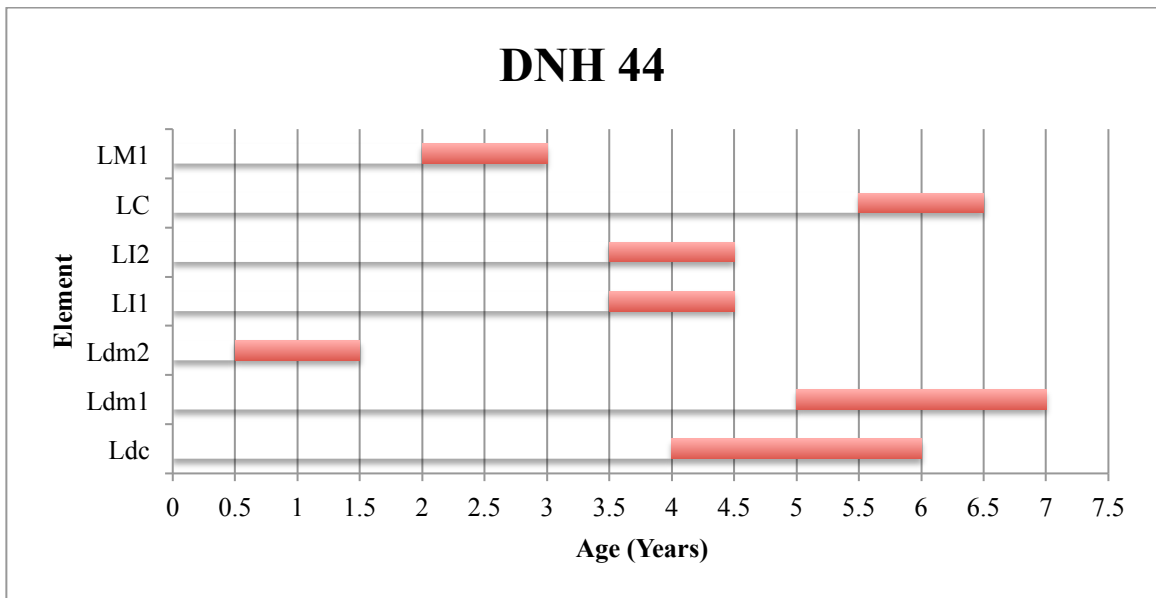
Table 5: Element-specific ages within DNH 44 interpreted based on a modern human model.
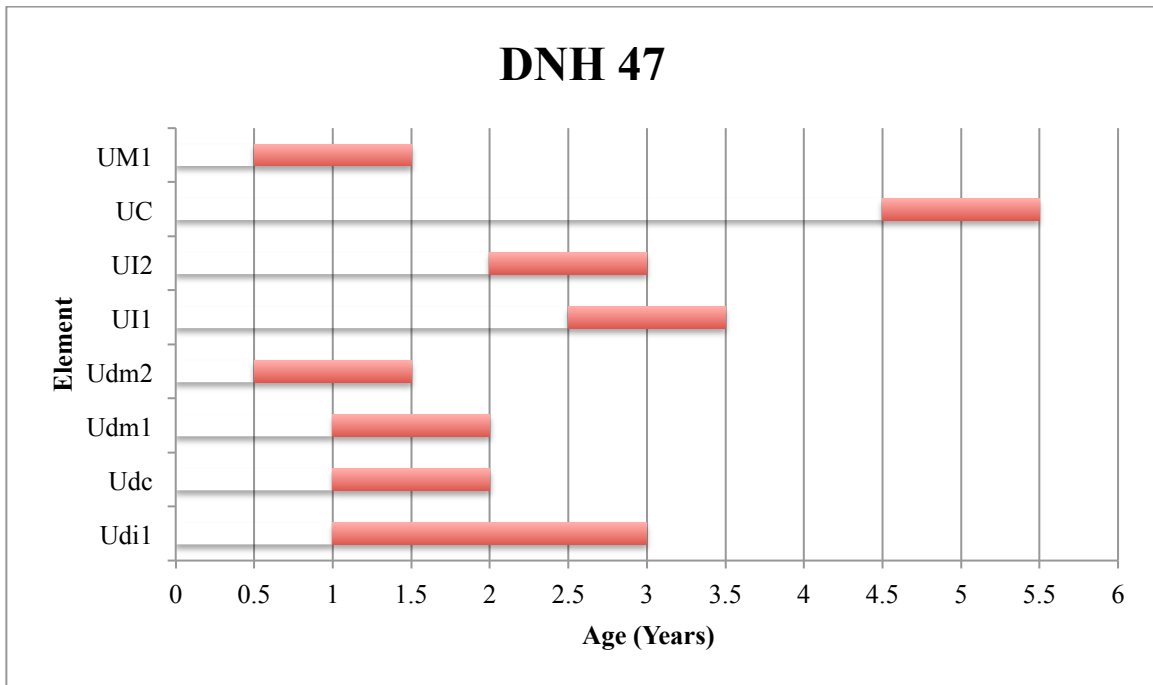
Table 6: Element-specific ages within DNH 47 interpreted based on a modern human model.
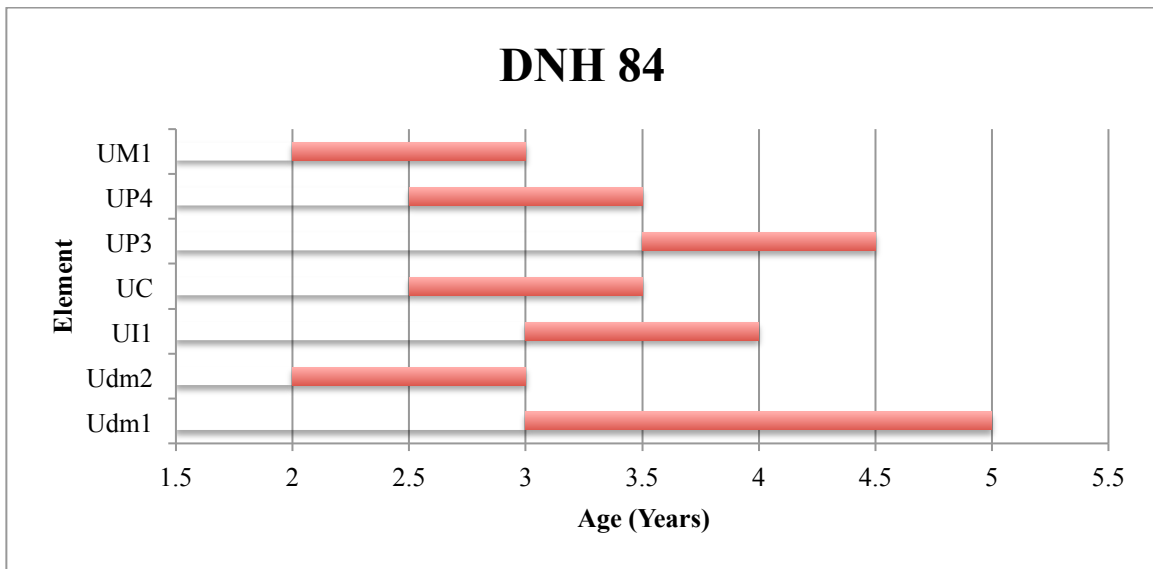
Table 7: Element-specific ages within DNH 84 interpreted based on a modern human model.
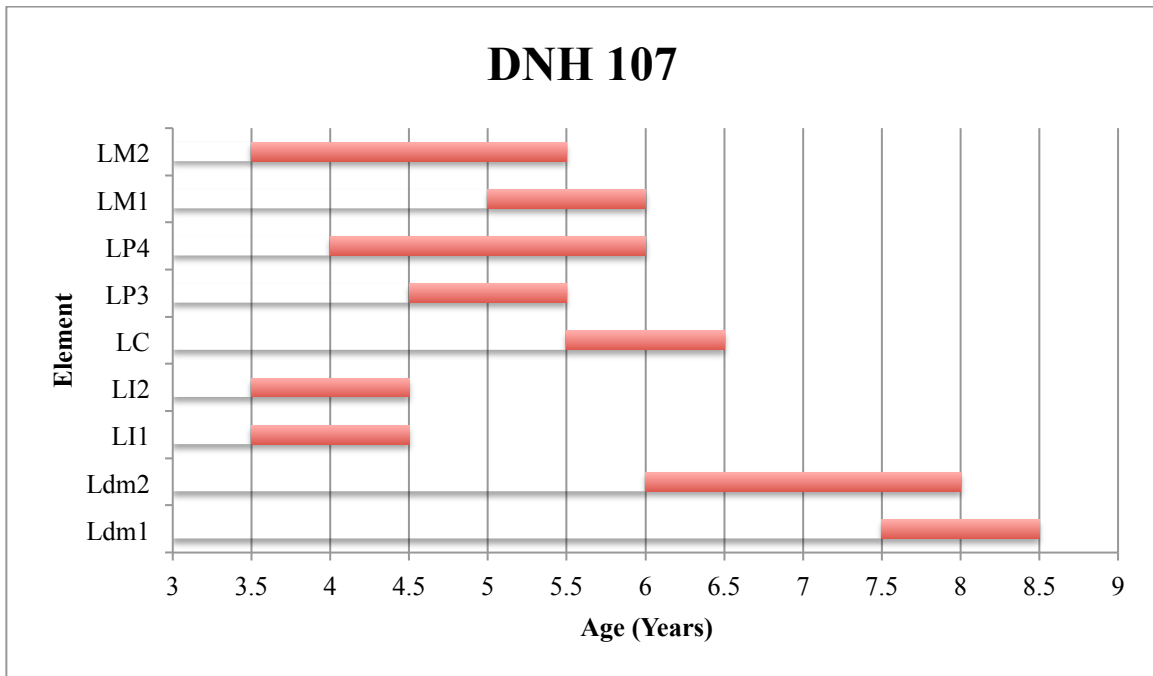
Table 8: Element-specific ages within DNH 107 interpreted based on a modern human model.
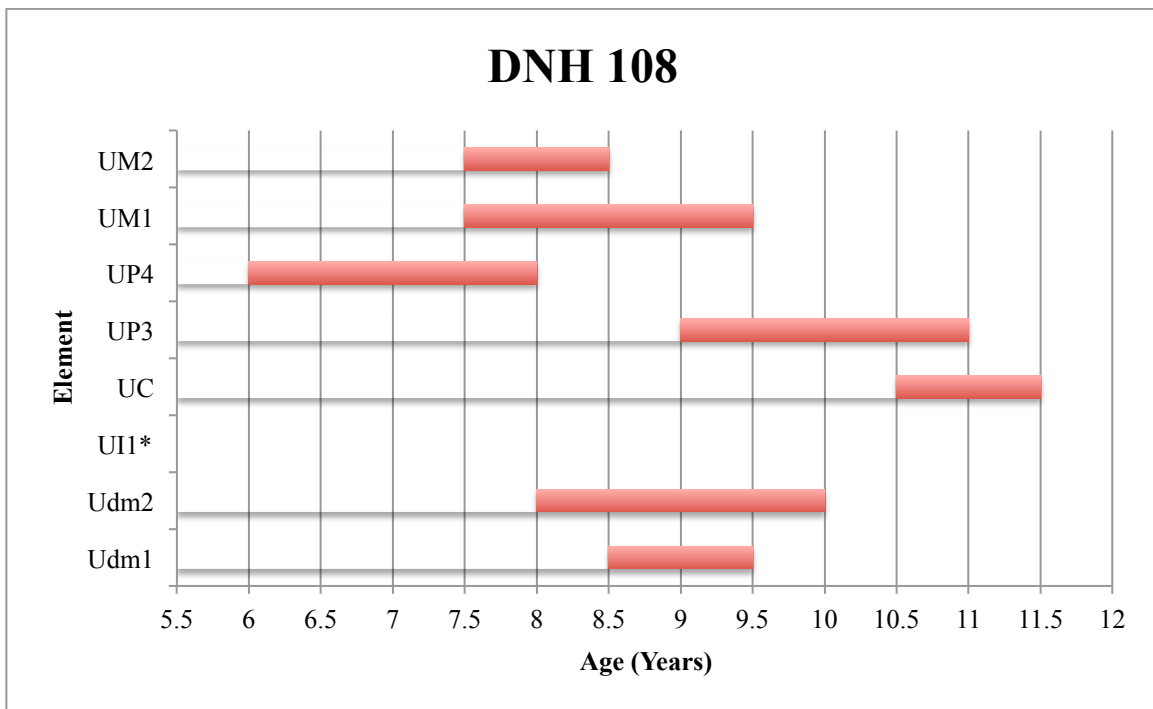
Table 9: Element-specific ages within DNH 108 interpreted based on a modern human model.

3.4 Conclusions

This comparative analysis demonstrated clearly the faults in using a modern human analogue for interpreting ages at death of early fossil hominins. These species quite evidently do not follow the same developmental patterns and rate as modern humans. This results in meaninglessly large age ranges attributed to these individuals.

The comparative data set produced in this study focused only on very young individuals, with DNH108 representing the oldest at 5.35/5.53 years (Smith et al. 2015). This was due in part, to the necessity to apply the histological methods used in Smith et al. (2015) to a very specific developmental stage range. This method can only be applied in individuals in which the M1 has reached crown completion but is not yet in functional occlusion. Additionally, the lack of methodological clarity in Mann's (1975) interpretation of wear stages and functional aging make interpretation and application to further assemblages impossible as the technique could not be consistently applied with any confidence.

4. Hominin MNI and Age Profile at Drimolen

4.1 Speciation and Descriptions

The Drimolen Main Quarry has yielded specimens attributed to *P. robustus* and the genus *Homo* (Moggi-Cecchi et al. 2010). Moggi-Cecchi et al. (2010) presented the descriptions and species attributions for the Drimolen hominin dental material: DNH 1 through DNH 83, excluding DNH 7, DNH 35, and DNH 47 (Table 10; Appendix 2). Descriptions and species attributions of DNH 84 through DNH 133, as well as DNH 7, DNH 35, and DNH 47, were completed by Dr. Jacopo Moggi-Cecchi and the author and are presented in Table 10 and Appendix 2. Alpha-taxonomic designation yielded three categories: *P. robustus*, early *Homo*, and indeterminate hominin. Specimens in the third category consist of either fragmentary material or specimens without distinct diagnostic morphology.

P. robustus			*Homo sp.*	Indeterminate
DNH1	DNH36	DNH84	DNH24	DNH11
DNH2	DNH40	DNH86	DNH35	DNH37
DNH3	DNH41	DNH87	DNH39	DNH38*
DNH4	DNH44	DNH88	DNH42	DNH61
DNH6	DNH46	DNH89	DNH45	DNH72
DNH7	DNH47	DNH90	DNH62	DNH85
DNH8	DNH49	DNH93	DNH67	DNH91
DNH10	DNH51	DNH94	DNH70	DNH92
DNH12	DNH52	DNH96	DNH71	DNH95
DNH14	DNH53	DNH97	DNH80	DNH105
DNH15	DNH54	DNH98	DNH83	DNH129
DNH16	DNH56	DNH101	DNH99	DNH132
DNH17	DNH57	DNH103	DNH100	
DNH18	DNH58	DNH104	DNH102	
DNH19	DNH59	DNH106		
DNH21	DNH60	DNH107		
DNH22	DNH68	DNH108		
DNH23	DNH73	DNH121		
DNH25	DNH74	DNH122		
DNH26	DNH75	DNH123		
DNH27	DNH77	DNH125		
DNH28	DNH78	DNH126		
DNH29	DNH79	DNH128		
DNH30	DNH81	DNH133		
DNH31	DNH82			

*Table 10: Species attributions of Drimolen hominin specimens; *DNH38 non-human primate (baboon)—Not included in MNI*

4.1.1 Methods

Specimens were examined using both a hand lens with 10X and 20X magnification and a low-powered binocular microscope. Descriptive terminology and comparative methodology follows Moggi-Cecchi (2010) after Robinson (1956), Tobias (1967, 1991), Grine (1984, 1989), and Moggi-Cecchi et al. (2006). A number of gross morphological features were examined for the purpose of species determination. These include:

- Overall occlusal outline (i.e. square, rectangular, rhomboidal)
- Angulation of enamel at the enamel-dentine junction (EDJ; i.e. 'bulbous' versus 'straight' lateral faces)
- Presence or absence of accessory cusps
- Angulation of cusps in relation to one-another
- Relative size and depth of fovea and other pitting
- Enamel thickness
- Bucco-lingual and mesio-distal dimensions

It should be noted that accessory cusps were only identified when a clear delineation from principle cusps denoted by a dividing fovea, was present (after Grine 1984). For example, the C7 accessory cusp is a morphological feature used to distinguish *Homo* from *P.* (Grine 1984; Figure 7). However, the identification of accessory cups and cuspulids is not standardised and concern has been raised about consistent identification and attribution (Grine 1984). Within the Drimolen assemblage, specimens showing a possible swelling at the point of C7 were attributed to *Homo* as this was not defined as a delineated cusp and other morphological features supporting this designation were present. This was done to maintain consistency with species attributions made within the Drimolen assemblage by Moggi-Cecchi et al. (2010).

Figure 7: DNH 2 showing delineated C7 as defined by Grine 1987.

4.1.2 Results

The taxonomic determinations resulted in 64 specimens being placed into the *P. robustus* category, 14 specimens into the early *Homo* category, and 12 specimens in the indeterminate category (Table 10). These determinations add 16 specimens to the previously published 48 *P. robustus*, 5 specimens to the previously published 9 *Homo*, and 8 specimens to the previously published 4 indeterminate categories (Appendices 2-4).

4.2 NISP and MNI

The majority of the hominin material recovered from the Drimolen Main Quarry consist of isolated dental material, with only 24 of the 111 accessioned dental specimens consisting of multiple elements. Postcranial material is preserved in the deposit in such low frequency (21 specimens) that these specimens do not affect the MNI determination.

Though originally attributed as a hominin and so given the appropriate accession prefix, DNH 38 has been reassessed as a non-human primate. Based on cuspal morphology, this specimen likely belongs to the genus *Papio* (Moggi-Cecchi et al. 2010). Consequently, this specimen has not been included in the NISP or the MNI.

4.2.1 NISP Methods

The Number of Individual Specimens Present (NISP) was calculated for the entire hominin assemblage inclusive of the years 1992 (Keyser et al. 2000) to 2015. As non-dental fragments less than two centimetres are unlikely to preserve sufficiently diagnostic morphology, they were excluded from this count. In addition material not definitely hominin was also excluded. As Drimolen is an extremely fossiliferous site (Figure 8), close spatial association with a known hominin specimen is insufficient grounds to attribute otherwise non-diagnostic fragments to hominin. That is, fossil material is dense and apparently lacking tight spatial association, often causing faunal and hominin remains to be recovered within centimetres of each other. Due to this, bone fragments not strictly diagnostic in and of themselves could not be confidently identified as hominin and were excluded from the NISP.
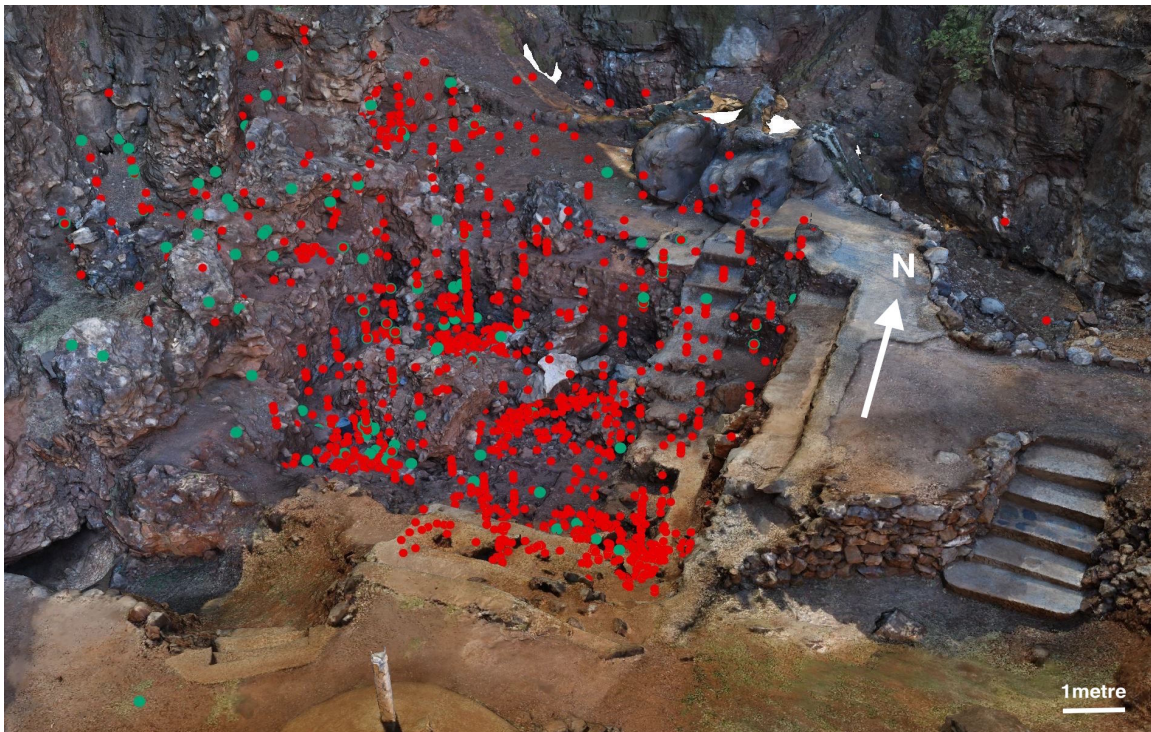
Figure 8: A subset of identifiable hominin and non-hominin fauna recovered from the Drimolen Main Quarry.

4.2.2 NISP Results

The total hominin NISP for all three taxonomic categories is 307 specimens. Of this, only 26 specimens represent non-dental material.

4.2.3 MNI Methods

Each of the three species categories listed above were then examined separately for the purposes of determining an MNI. For the purposes of presenting the most conservative MNI, it was assumed that the postcranial material belonged to an individual otherwise represented by a craniodental specimen. Cranial material not directly associated with dental specimens was treated in the same manner. Each dental specimen was then examined under a certain set of criteria including:

- Developmental stage
- Occlusal wear stage
- Interproximal faceting
- Crown size
- Enamel thickness
- Micro- and macro-morphology specific to the individual element (i.e. perikymata spacing, hypoplastic pitting, irregularities and faults)
- Preservation and staining
- Spatial data (used with caution due to issues discussed previously)

These variables were considered for the purposes of producing a comparative MNI (or cMNI; Pickering 1999).

4.2.4 MNI Results

Applying the MNI methodology detailed above across the three species categories resulted in eight individuals in the 'Indeterminate Hominin" category, nine individuals in the '*Homo sp.*' category, and 49 individuals in the '*P. robustus*' category (Table 11). See Appendix 3 for internal comparisons and reasoning.

Species	Individual					
P. robustus						
	1 & 4	2 & 49	3 & 41	6	7	8
	10, 16, & 29	12	14 & 17	15, 18, & 19	21 & 27	22
	25 & 77a&b	26 & 106	28 & 59	30 & 23	31, 88, & 94	36
	40	44 & 87	46	47	51	52
	53	56 & 57	58 & 86	60 & 82	68	73
	74	75	78, 89, & 107	79a&b	81 & 84	90
	93	96	97	98	101	103
	104	108	121	122	125	126
	133					
Homo sp.						
	24	35	39, 45, & 100	42 & 62	67, 70, & 71	80
	83	99	102			
Indeterminate						
	11, 37, & 61	85 & 105	72	91	92	95
	129	132				

Table 11: MNI determinations of the Drimolen hominin assemblage.

4.3 Relative Age Seriation

As discussed in detail in previous chapters, chronological ages must be assigned to hominin individuals for the purposes of a demographic assessment. Issues with prior methodologies involving aging these extinct species using modern analogues, human or ape, have been discussed in Chapters 3 and 4. For this reason, the Drimolen assemblage has been seriated based on relative age.

4.3.1 Methods

Relative age was assessed based on multiple criteria including (Appendix 4):

- Developmental stage
- Eruption stage
- Occlusal and interproximal wear stage

Categorical divisions reflecting eruption stages were used first to determine a preliminary age seriation. Dental elements were determined to be in occlusion if any form of cusp polishing or faceting was observed. These observations were made using both a hand lens with 10X and 20X magnification and a low-powered binocular. These broad categories were then divided based on wear stage. These wear categories could not, of course, be applied to anterior teeth. Instead, incisors and canines were assessed based on relative dentine exposure size and estimated loss of crown height. All categorical determinations were based on visual assessment.

Categories were as follows (defined in Table 12):

- dm1 erupted
- dm2 erupted
- Light wear on dm1
- M1 erupted
- Light wear on dm2
- Heavy wear on dm1
- Heavy wear on dm2
- M2 erupted
- P3 erupted
- P4 erupted
- M3 erupted
- One dentine exposure on M2
- Flat occlusal surface of M3
- Two dentine exposures on M2

- One dentine exposure on M3

- Three dentine exposures on M2

- Large dentine exposure on M3
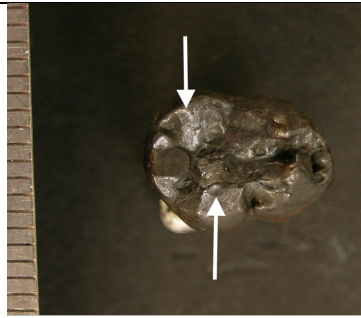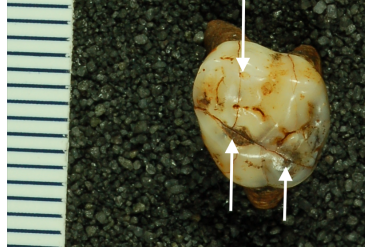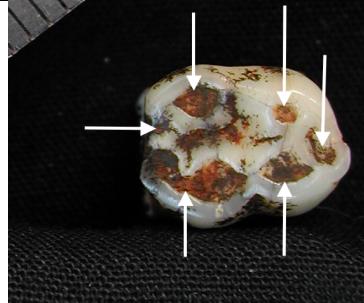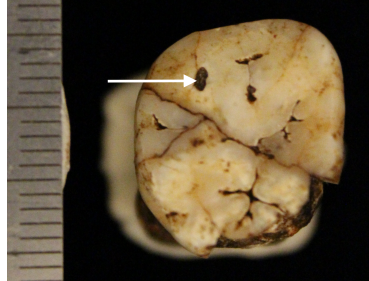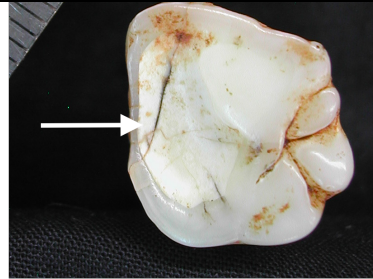
Stage	Defining Criteria	Example
Newly erupted	Cuspal polishing; Extremely light enamel faceting	
Light wear on deciduous element	One or more small dentine exposures	
Heavy wear on deciduous element	Multiple large dentine exposures; One very large conjoining dentine exposure	
One/Two/Three dentine exposure(s) on permanent element	Dentine exposure(s) matching the count stated in the category	
Large dentine exposure on M3	Large conjoining dentine exposure, extending to more than one cusp	

Table 12: Dental wear category visual assessment examples.

More complete specimens were used to gauge the stages of different elements relative to one another within a single individual for the purposes of placing isolated dental remains within the seriation. As preliminary assessment indicated age gaps not represented in the *P. robustus* material preserved at Drimolen, a sample of *P. robustus* from Swartkrans and Kromdraai (SK 6, 11, 12, 13/14, 23, 25, 34, 46, 48, 49, 52, 61, 62, 63, 64, 65/65a/67, 79, 83, 3978, 852/839, 858/883/861, TM 1600, 1601, KB 5223/5383) was examined for comparative purposes. These specimens were examined in the same manner as the Drimolen collection for the purposes of potentially identifying specimens that fit within the age gaps seen in the Drimolen *P. robustus* assemblage. The addition of the Swartkrans sample also increases the number of individuals consisting of more than one dental element. The addition of the Swartkrans individuals represented by more than one element increases the sample size, allowing for a finer-grained assessment of individual variation with regards to formation and eruption timing.

4.3.2 Results

Species	Individual	Relative Dental Stage
P. robustus		
	125	No Dentition in Occlusion
	47	Deciduous Dentition Only
	36	Deciduous Dentition Only
	31, 88, & 94	Deciduous Dentition Only
	44 & 87	Deciduous Dentition Only
	49 & 2	Deciduous Dentition Only
	56 & 57	Deciduous Dentition Only
	84 & 81	Deciduous Dentition Only
	96	Deciduous Dentition Only
	126	Deciduous Dentition Only
	103	Mixed Dentition

	107, 89, & 78	Mixed Dentition
	133	Mixed Dentition
	60 & 82	Mixed Dentition
	93	Mixed Dentition
	98	Mixed Dentition
	108	Mixed Dentition
	101	Mixed Dentition
	79a&b	Mixed Dentition
	30 & 23	Mixed Dentition
	90	Mixed Dentition
	46	Mixed Dentition
	106 & 26	Permanent Dentition Only
	121*	Permanent Dentition Only
	75	Permanent Dentition Only
	22	Permanent Dentition Only
	28 & 59	Permanent Dentition Only
	74	Permanent Dentition Only
	12	Permanent Dentition Only
	52	Permanent Dentition Only
	73	Permanent Dentition Only
	8	Permanent Dentition Only
	1 & 4	Permanent Dentition Only
	10, 16, & 29	Permanent Dentition Only
	41 & 3	Permanent Dentition Only
	128 & 54	Permanent Dentition Only
	7	Permanent Dentition Only
	122	Permanent Dentition Only
	68	Permanent Dentition Only
	6	Permanent Dentition Only
	51	Permanent Dentition Only

	21 & 27	Permanent Dentition Only
	104	Permanent Dentition Only
	15, 18, & 19	Permanent Dentition Only
	86 & 58	Permanent Dentition Only
	25 & 77a&b	Old Adult
	14 & 17	Old Adult
	40	Old Adult
	97	Old Adult
	53**	–
Homo sp.		
	102	Deciduous Dentition Only
	24	Deciduous Dentition Only
	83	Deciduous Dentition Only
	42 & 62	Deciduous Dentition Only
	67, 70, & 71	Deciduous Dentition Only
	35	Deciduous Dentition Only
	99	Deciduous Dentition Only
	39, 45, & 100	Mixed Dentition
	80	Permanent Dentition Only
Indeterminate		
	95	–
	85 & 105	–
	132	–
	91	–
	61, 37, & 11	–
	129	–
	72	–
	92	–

Table 13: Relative age seriation of Drimolen hominin assemblage with dental eruption stage.

Relative age seriations of each taxonomic category can be found in Table 13. The 14 specimens in the early *Homo* category likely represent nine individuals as determined through the MNI assessment discussed above. Approximately 78% (seven individuals) of the early *Homo* category consists of very young individuals with only deciduous dentition in the mouth. Those with mixed dentition and those with permanent dentition only represent 11% (one individual) each Table 15. The 64 *P. robustus* specimens likely represent 49 individuals. 2% (1 individual) of these individuals have no dentition in occlusion and 19% (9 individuals) fall into the Deciduous Only age range. The Mixed Dentition group contains 21% (10 individuals) and the Permanent Only group contains 50% (24 individuals) with 4% (8 individuals) falling into the Old Adult category (Table 14). It should be noted that DNH 53 was not placed specifically into the age seriation. Atypical wear, likely due to misalignment in the dental arcade, made anything more than placement in the permanent-only category impossible (Figure 11). Additionally, DNH 121, despite representing a dm2, has been placed into the permanent-only category. As discussed in the description of this specimen (Appendix 2), this element has likely already been shed, indicating that the individual to which it belonged would only have permanent dentition in the mouth.

Drimolen *P. robustus*		
Dental Stage	**No. Individuals**	**% Pop. Represented**
No Dentition in Occlusion	1	2
Deciduous	9	19
Mixed	10	21
Permanent	24	50
Old Adult	4	8
Total	**48**	

Table 14: Wear category attribution of the Drimolen P. robustus *palaeo-population.*

Drimolen *Homo*		
Dental Stage	**No. Individuals**	**% Pop. Represented**
No Dentition in Occlusion	0	0
Deciduous	7	78
Mixed	1	11
Permanent	1	11
Old Adult	0	0
Total	**9**	

Table 15: Wear category attribution of the Drimolen Homo *palaeo-population.*

Figure 9: DNH 53; Interproximal wear facets indicative of malocclusion

As is suggested by separating out an 'Old Adult' category, multiple age gaps are possibly visible within the Drimolen *P. robustus* population. This will be discussed further in the subsequent chapters examining formation, eruption, and wear patterns of this species.

Two significant patterns are made evident by these categories. Wear categories were determined based on the most consistently applicable pattern. These categories are not consistent across element (e.g. 'three dentine exposures on M2' versus 'large dentine exposure on M3') as different elements appear to wear differently. This is likely influenced by both specific enamel cap and dentine horn morphology and specific biomechanical stress. These trends are discussed in more detail in Chapter 7. Additionally, it becomes evident that certain age groups are not represented within the Drimolen assemblage. This pattern is discussed in more detail in Chapter 8.

4.4 Histological Ages

As discussed in Chapter 4, Smith et al. (2015) presents chronological ages at death, determined through histological methods, for particular hominin specimens. This approach allows researchers to avoid errors inherent in using extant analogues. However, the sample used by Smith et al. (2015) only represents the younger portion of the age profile, as the method can only be applied to individuals with M1s at crown completion but not yet in wear. The oldest specimen assigned a chronological age sits early on in the mixed dentition category at 5.35/5.53 years (Smith et al. 2015).

4.4.1 Methods

Exact ages presented by Smith et al. (2015) were not taken into account when relatively seriating the Drimolen assemblage. This was done to avoid external bias of the relative seriation method. Instead, these ages were used as a test of the relative aging technique. Once the relative seriation was determined through the methodology discussed above, the chronological ages presented by Smith et al. (2015) were applied to the seven specimens to assess the accuracy of the seriation.

4.4.2 Results

Two Drimolen individuals sampled by Smith et al. (2015) were attributed to early *Homo* and five Drimolen individuals were attributed to *P. robustus*. All seven individuals were assigned ages that fell into appropriate relative seriation (Table 16). This support the

seriation as a whole as well as supporting the previously mentioned notion that a non-time averaged assemblage would help to limit odontogenetic variability (as discussed in Grine 1987.

Species	Individual	Smith et al. (2015) Ages
P. robustus		
	125	
	47	0.67-0.77 years
	36	
	31, 88, & 94	
	44 & 87	1.70 years (DNH 44)
	49 & 2	
	56 & 57	
	84 & 81	2.24 years (DNH 84)
	96	
	126	
	103	
	107, 89, & 78	4.82 years (DNH 107)
	133	
	60 & 82	
	93	
	98	
	108	5.35/5.53 years
	101	
	(Older specimens excluded)	
Homo sp.		
	102	
	24	
	83	0.52 (7)/0.59 (8)
	42 & 62	

	67, 70, & 71	
	35	2.18 years
	99	
	39, 45, & 100	
	80	

Table 16: Relative age seriation of Drimolen hominin material in comparison to Smith et al.'s (2015) histological ages.

5. Formation and Eruption Patterns

As previously discussed in Chapters 2 and 3, using analogues to interpret a fossil individual's age based on dental patterns is problematic. Notwithstanding that chimpanzee developmental patterns are often used as analogues for extinct species due to their relative phylogenetic closeness to *H. sapiens*, it is generally accepted that the ontogenetic profile of extinct human ancestors is likely to have been intermediate between *H. sapiens* and chimpanzees (see discussion in Chapter 2). Therefore, an accurate interpretation of species-specific dental development is crucial to the understanding of extinct species. Not only are exact ages at death important to demographic interpretations (discussed further in Chapter 7), but dental development patterns have been shown to correlate directly with other characteristics such as adult brain size, lifespan, and life-history traits (i.e. age at weaning, age at first reproduction, etc.; see, for instance, Dean et al. 2001 as well as discussion in Chapter 2). It has been hypothesised that this correlation is due to the influence of adaptive strategy on life-history (Bronikowski et al. 2010).

As discussed in Chapter 2 and demonstrated in Chapter 3, histological methodologies are being utilised increasingly to determine age at death without reliance on extant analogues. Studies such as Smith et al. (2015) have assigned chronological ages to a sample of hominin individuals as well as having presented ages of dental formation stages such as mineralization and crown completion. The histological method applied by Smith et al. (2015), however, can only be applied to individuals at a particular stage of odontogenesis (M1 crown complete, not yet erupted). This therefore limits the data that can be collected. That is, if the odontogenetic stages in question do not occur in certain elements within the age range assessed, determination of these stages becomes problematic. This study proposes the use of relative age seriation to supplement data presented through Smith et al.'s (2015) histological study. While exact chronological ages cannot be determined in this way, the aim of this assessment is to identify age *ranges* in which these stages occur. Data gathered from the relative age seriation has been used here to supplement odontogenetic data presented by Smith et al. (2015) for the

purposes of determining a more fulsome pattern of dental development within *P. robustus* at Drimolen.

5.1 Methods

Based on the relative age seriation of the Drimolen *P. robustus* sample completed as part of this study, a preliminary formation and eruption pattern specific to this species was developed. The stages of formation (after Demirjian et al. 1973; Table 17) and eruption (after Ubelaker 1979), wear, and root resorption of elements belonging to individuals containing multiple dental elements were used to estimate the pattern in which development occurred. That is, elements within an individual displaying a more advanced developmental stage was interpreted as having begun formation sooner than those at a less advanced stage. Equally, dental elements displaying heavier wear (Table 12) than equivalent elements were interpreted as having erupted earlier. The presence of root resorption of deciduous dentition was interpreted as indicative of in-crypt permanent dentition. More advanced root resorption was taken as indicative of the deciduous element approaching the point of shedding and the permanent element approaching eruption.

Wear is discussed here in relative terms only for the purposes of determining eruption order and will be examined in more detail in Chapter 6. Relative wear was assessed through visual observation as in the relative seriation (Table 12; as applied in Chapter 4). Elements were considered newly erupted when they displayed cusp polishing or light enamel faceting. In cases where specimens given exact ages included elements showing the aforementioned stage of wear, these elements were recorded as erupting at approximately that age. In cases where eruption occurred in a specimen lacking an exact age, eruption age was recorded as a range depending on where the individual was placed relative to the aged specimens (Table 18).

Formation Stage	Markers
Stage A	Calcification of the cusp tips, however have not yet united in multiradicular teeth
Stage B	Cusp tips unite to form a regularly outlined coronal surface
Stage C	Crown formation extends towards cervical region; dentinal deposition and pulp chamber are observable
Stage D	Crown formation is complete; pulp chamber is curved in uniradicular teeth and exhibits a trapezoidal shape in multiradicular teeth
Stage E	Walls of pulp chamber exhibit straight lines in uniradicular teeth; initial formation of radicular bifurcation in molars; root length is less than crown height in all teeth
Stage F	Walls of pulp chamber for isosceles trianlges in uniradicular teeth; molar roots are more definate and funnel shaped; rooth length is equal to or greater than crown height in all teeth
Stage G	Root length is nearly complete, however its apical end remains open
Stage H	Apical end of the root is closed; the periodontal membrane has uniform width around the root and apex

Table 17: Dental development stages; After Demirjian (1973)

Developmental Stages used in this assessment, inclusive of stage of root development at the time of eruption, follow Demirjian (1973; Table 17). Initiation times were calculated independently of those presented by Smith et al. (2015) to supplement the data provided. Smith et al. (2015) determined formation times and age at initiation using histological methods. This study assessed these developmental stages through visual observation of the fossil material, in the same way eruption times were determined. This allowed for estimates to be made in regards to dental elements not addressed by Smith et al. (2015). In instances where data was available, results yielded by this method where then compared to those presented in Smith et al. (2015).

Element	Crown Complete MIN	Crown Complete MAX	Eruption MIN	Eruption MAX	Root Complete MIN	Root Complete MAX	Root Stage at eruption
di1	–	<0.67	–	<0.67	–	<0.67	>E
di2	–	<0.67	–	<0.67	>0.67	<1.7	<G
dc	–	<0.67	–	<0.67	>0.67	<1.7	~F
dm1	–	<0.67	–	<0.67	>0.67	<1.7	<F
dm2	–	<0.67	>1.7	<2.24	–	~2.24	~G
I1	–	–	>4.82	<5.35/5.53	>4.82	<5.35/5.53	>E
I2	–	4.82	–	–	>4.82	–	>E
C	2.79	3.15	–	~5.35/5.53	–	>5.35/5.53	~F
P3	3.74	5.35/5.53	–	–	–	>5.35/5.53	>F
P4	4.82	5.35/5.53	–	–	–	>5.35/5.53	>E
M1	1.6	2.53	–	~4.82	>4.82	<5.35/5.53	~E
M2	4.22	5.06	–	–	–	>5.35/5.53	–
M3	–	–	–	–	–	–	–

Table 18: Conglomerated dental development data for Drimolen P. robustus; data drawn from Smith et al. (2015) recorded in red.

5.2 Results

Proposed dental development patterns are presented in Table 18.

5.2.1 DNH 47 (Figure 10)

By 0.67-0.77 years of age (approximately 7 months; Smith et al. 2015), the di^1, dm^1, di_2, dm_1, and possibly the d^c are in occlusion. While wear cannot be assessed on the d^c and di^1 due to breakage, both the dm^1 and the dm_1 show enamel faceting, indicating they had recently erupted. The di_2 already shows dentine exposure along the incisal edge, indicating that it had been in occlusion for a significant amount of time. Despite being in functional occlusion, both the di_2 and the d^c do not yet have completed roots (Stages G and F, respectively). At this age, the dm^2 is at developmental Stage E-F, while the I^1 and M^1 are both at Stage B-C. All three elements are unerupted.

Figure 10: DNH 47

5.2.2 DNH 44 (Figure 11)

By 1.70 years of age (approximately 1 year and 8 months), the d^c shows a small degree of root resorption. The dm_1 shows three dentine exposures while the dm_2, I_2, and M_1 are yet unerupted. It must be noted that the large disparity between the dm_1 and dm_2 eruption times evident in this specimen suggests atypical attrition as it is not evident in other individuals within the Drimolen *P. robustus* assemblage.

Figure 11: DNH 44

5.2.3 DNH 84 (Figure 12)

By 2.24 years of age (approximately 2 years and 3 months), the dm^1 and dm_1 show two dentine exposures and the dm^2 is newly erupted, showing light enamel faceting. As this is

more consistent with the sample as a whole, it is possible that the dm_1 of DNH 44 erupted at an abnormally young age. Both the I^1 and M^1 are unerupted showing developmental Stages C-D and D-E, respectively.

Figure 12: DNH 84; M^1 only

5.2.4 DNH 107 (Figure 13)

By 4.82 years of age (approximately 4 years and 10 months), the left and right dm_1s both show very heavy wear and a high degree of root resorption, while the left and right dm_2s show significantly less wear and slight root resorption. The I_1 shows incomplete roots at Stage E while the Right and left $_c$s and I_2s have reached crown completion (Stage D-E). The M_1 is newly erupted and the M_2 is not yet at crown completion (Stage B-C).
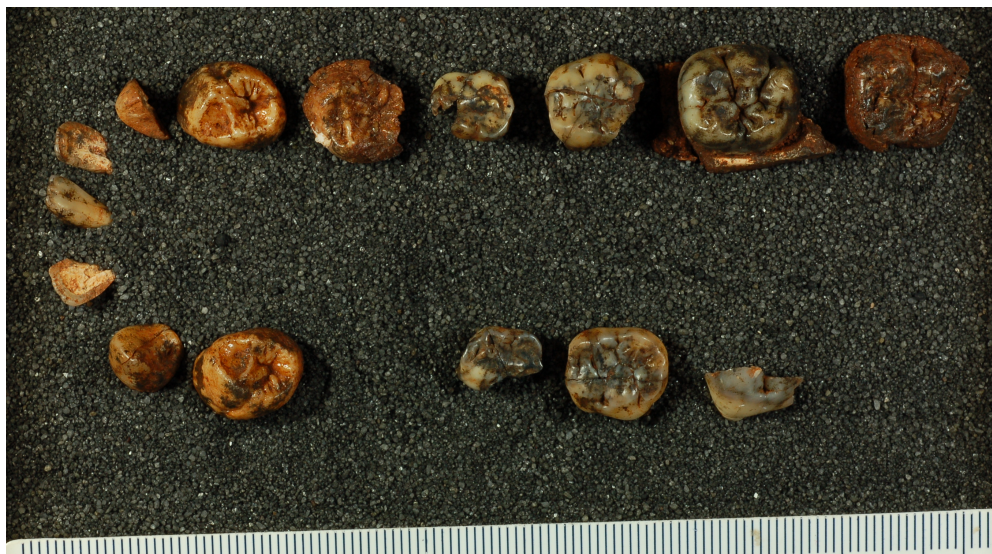
Figure 13: DNH 107

5.2.5 DNH 108 (Figure 14)

By 5.35/5.53 years of age (approximately 5 years and 4 months/5 years and 6 months), the dm^1 is likely close to shedding, and the left and right dm^2s also shows significant, if slightly less, root resorption. The left and right ^{C}s are newly erupted though they have not yet reached root completion (Stage F). The left and right P^3s, P^4s, and the right M^2 are all at crown completion though the P^4s are slightly less advanced (showing Stage D-E as opposed to Stage E-F).

The available data, drawn from both aged specimens and those relatively seriated, suggests that most dental elements come into functional occlusion with incomplete roots at Stages E or F. In the case of the dm1, it seems common for the element to be in occlusion long enough to show dentine exposures before the roots have completed. Both the deciduous and permanent dentition appear to erupt in a slightly different order than modern *H. sapiens*. Deciduous dentition appears to erupt in the following order: di1, followed by di2, followed by dc and dm1 at similar times, and lastly dm2. The permanent dentition exhibit the following order: M1, followed by I1, followed by I2 and C at similar times, followed by P3 and M2 at similar times, followed by P4, and lastly M3. However, DNH 106 does indicate that the M2 may erupt just prior to the P3. Timing between the eruption of sequential elements, however, is likely not equivalent.

Figure 14: DNH 108

5.3 Discussion

5.3.1 Deciduous Dentition

As discussed in Chapter 3, when utilised to assess deciduous dentition as opposed to permanent dentition, the application of a modern human analogue to *P. robustus* individuals yielded a more accurate, though still erroneous result (Table 2). It would therefore be expected that the developmental pattern of deciduous dentition would be more similar between modern human and *P. robustus* than the permanent dentition. If this hypothesis is supported, it would suggest an extended childhood period in *P. robustus*. Comparison between *P. robustus* dental patterns presented here and those presented by Gustafson and Koch (1974) and Massler and Schour (1946) suggest that the deciduous dentition of *P. robustus* erupt much earlier than that of modern *H. sapiens*. While the order in which they erupt is consistent between the two species, the rate of eruption of *P. robustus* deciduous dentition cannot be determined with the current data set, as shown in this study, and so a comparison cannot be drawn. Eruption timing of deciduous dentition may be equivalent to that seen in *Papio* species (Smith et al. 1994) however, element specific information is not available. A comparison to the development of deciduous dentition in chimpanzees cannot be conducted, as specific data is available for permanent elements only (Nissen & Riesen 1964).

5.3.2 Permanent Dentition

5.3.2.1 Mineralisation

No data is presented either by this study or within Smith et al. (2015) in regards to mineralisation times of the I2, P4, or M3 in *P. robustus* as the specimens within the sample did not allow for assessment. Crown mineralisation times of the other permanent elements appear similar between *P. robustus* and modern *H. sapiens*. Though the M2 may begin mineralisation earlier (2.01-2.43 years; Smith et al. 2015) in the former, the I1 may begin slightly later (0.30-0.69 years; Smith et al. 2015). The age range for initiation of the chimpanzee I1 sits within the age range of *P. robustus* (Kuykendall 1996). The C of *P. robustus* appears to begin mineralisation later than the chimpanzee on average

(0.55-0.90 years; Smith et al. 2015). The mineralisation of the male chimpanzee however begins later, and the *P. robustus* range overlaps only with the youngest end (Kuykendall 1996). Smith et al. (2015) does not present a *range* for initiation timing of the P3, however the age of 1.63 years presented sits within the range of chimpanzee (Kuykendall 1996). An initiation age for the chimpanzee M1 is not presented, however unless the chimpanzee mineralisation is extremely slow, the *P. robustus* M1 likely begins mineralisation at a younger age (Kuykendall 1996). Data presented here indicates that the M2 of *P. robustus* begins mineralisation on average a year later than that of the chimpanzee (Kuykendall 1996).

5.3.2.2 Crown Completion

Precise crown completion ages calculated using data presented by Smith et al. (2015) are only available for the C, P3, M1, and M2 of *P. robustus* while crown completion time of other elements, excluding the I1, have been estimated using the data generated in this study.

The age of crown completion presented for the I2 (4.82 years) sits within the range of chimpanzee (Kuykendall 1996). The C appears to reach completion far sooner in *P. robustus* (2.79-3.15 years; Smith et al. 2015) than in chimpanzee (Kuykendall 1996). This is not unexpected as the chimpanzee canine, particularly upper canines of males, are absolutely larger than those of *P. robustus* (Swindler 1976) and so would be expected to require a longer period of formation. The age ranges presented for the P3s and P4s (4.82-5.35/5.53 years) of *P. robustus* and chimpanzee are nearly identical, with the P4 range in chimpanzee shifted slightly older (Kuykendall 1996). The M1 age ranges are nearly equivalent as well, with the *P. robustus* (1.6-2.53 years; Smith et al. 2015) showing a slightly older range (Kuykendall 1996). The age range presented for the *P. robustus* M2 is much shorter (4.22-5.06 years; Smith et al. 2015) and sits within that of the chimpanzee (Kuykendall 1996).

5.3.2.3 Eruption

As is the case with the deciduous dentition, eruption of permanent dentition in *P. robustus* may be similar to that of *Papio* species, however more element specific detail is required before this can be assessed (Smith et al. 1994). Age ranges of *P. robustus* eruption timing that have been proposed by Smith et al. (2015) and as part of this study are of limited utility. As only a small sample of *P. robustus* individuals (DNH 44, 47, 84, 107, & 108) was suitable for comparison to each other due to the fragmentary nature of the other young individuals, the estimates of age ranges are quite broad and subject to a large degree of error. Future study refining these age ranges would be crucial to dental development interpretation. Despite this, preliminary comparison suggests the I1 age range overlaps largely with that of chimpanzee while the C of the chimpanzee erupts much later (Nissen and Riesen 1964).

The ~7 month old individual (DNH 44) containing an M1 at Stage B-C and the ~2 year and 3 month old individual (DNH 84) containing an M1 at Stage D-E, suggests either a very slow development or a highly variable development of this element. Based on initiation times and direct observation, M1 mineralisation seems to begin at the time of, or just prior to, dm1 eruption. As it is assumed M1 mineralisation begins at the time of birth, it would be expected that the dm1 erupts shortly thereafter. The youngest individual given an exact age is ~0.67-0.77 years (Smith et al. 2015) and contains a dm1 with enamel faceting indicating it had erupted recently, supporting this hypothesis. M1 and I1 crown completion appear to occur at similar times despite the disparity in eruption times. M1 eruption seems to occur just prior to M2 crown completion. P3 and C crown completion seem to occur at a similar time to M1 eruption. The large disparity consistently documented between M2 wear and M3 wear may be due to a significant amount of time between eruption, difference in attrition rates due to loading differences, or a combination of the two.

6. Wear Pattern Assessment

As discussed in Chapters 2 and 3, the use of great ape or modern human analogues for interpreting age at death of hominin individuals is a problematic methodology. Issues detailed previously in regards to inequivalent life-histories, adaptive strategies and behaviours, and developmental suites (Smith 1994) also prevent these analogues from applying to the interpretation of wear in hominin individuals. Established wear patterns of extant species cannot be utilised to accurately interpret wear stages of an extinct species' dentition. Wear is dependent on diet, enamel thickness, dental arcade shape, dental formula, occlusal stress pattern, and developmental patterns, among other factors (Lee-Thorp et al. 2010; Fung 2013). While it has been argued that some of these variables align with certain extant species (see discussion in Chapter 3), no analogue exists that matches all of them. For these reason, extant models were not used in this study. The previously discussed relative seriation instead used wear stages only in comparison within the sample and not to assign an exact age to the specimens.

A new approach for assessing dental wear will be presented here. This methodology will test a quantifiable technique for interpreting occlusal wear patterns on post-canine teeth. A predictable and quantifiable pattern of occlusal wear would be a useful tool in determining age at death for specimens consisting of isolated dentition as well as for specimens not suitable for histological age methodologies. Determining formation and eruption patterns are crucial to determining age at death of fossil individuals, but this technique only extends to the age at which all dental elements are in occlusion. Building on these patterns, a known rate of wear would facilitate assessment of older individuals, as is the case in extant species, including modern humans.

6.1 Methods

This preliminary study established a novel method for quantifying dentine exposure due to attrition on the occlusal surface of post-canine dentition. Anterior elements could not be assessed as, once occlusal enamel is lost, further wear becomes evident through loss of crown height as opposed to expanding dentine exposures. Without knowing the starting

crown height of the specimens, results would be inaccurate. As molars preserve more frequently in the fossil record, the study progressed using a sample of these elements.

This study used undistorted photos to preserve and record original scale of the occlusal surface for assessment. The workflow was as follows:

- Images were imported into ImageJ 1.49v (Abramoff et al. 2004; Schneider et al. 2012)
- The scale was set independently for each specimen using the Straight Line tool on an in-picture scale bar (Figure 15)
- The occlusal surface was defined using the Polygon Selection tool (Figure 16)
- Any dentine exposures were then defined using the Polygon Selection tool (Figure 17)
- Selected areas were then calculated using the Analyse tool, Measure

Figure 15: Set scale with line tool

Figure 16: Occlusal outline selection with polygon selection tool
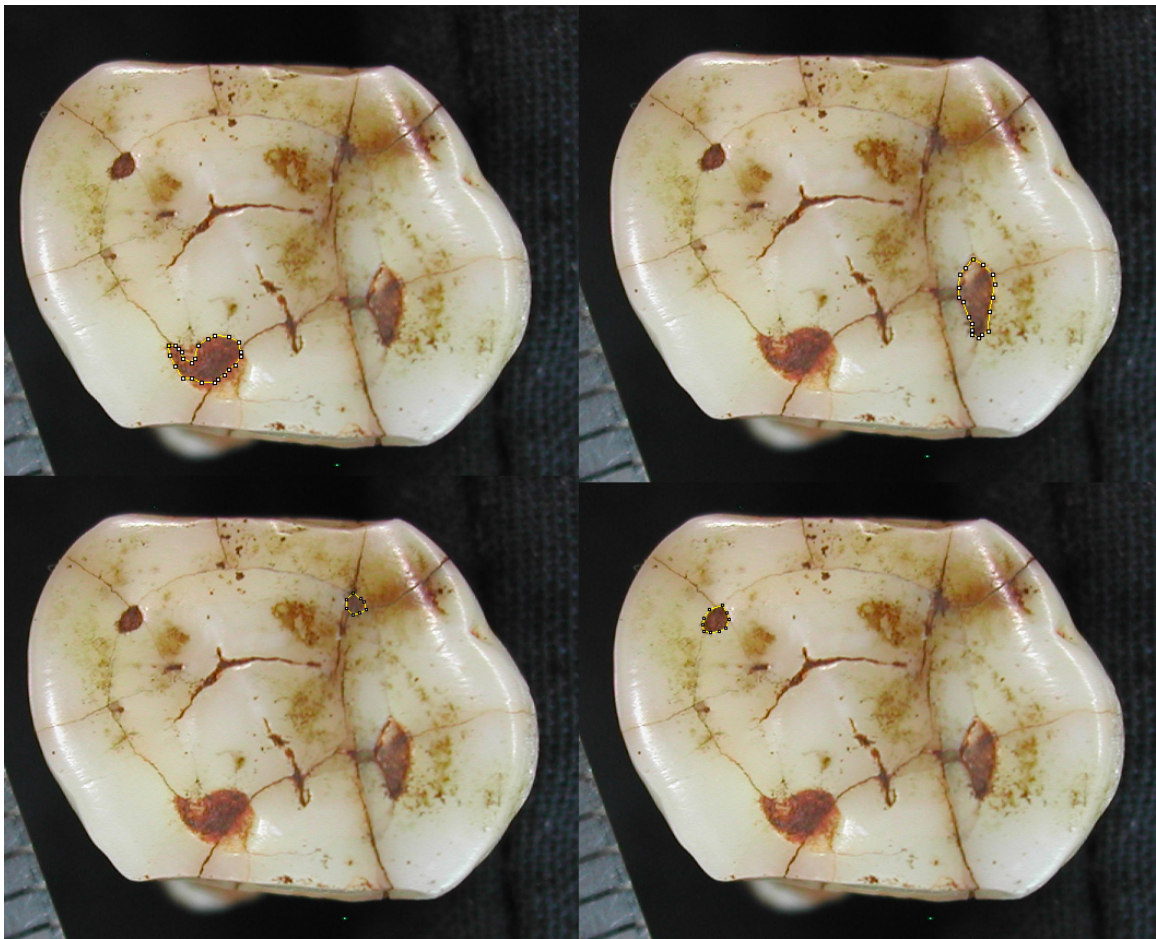
Figure 17: Dentine exposure selection with polygon selection tool

For the purposes of this study, the occlusal surface was defined as the region of the element on which at least minimal wear (polish) could be identified. Where necessary, cast material was used to assist in this identification. Sloping enamel surrounding dentine exposures was not included in the measurements. Each area measurement was taken ten times and the average result was used for analysis.

The percentage of occlusal surface occupied by dentine exposure was then calculated:

% Wear = (Area of Occlusal Surface/Area of Dentine Exposure) x 100

Two hypotheses were tested through this study:
- Chronologically older individuals will exhibit a higher percentage of wear on equivalent dental elements than chronologically younger individuals.
- Percentage of wear will decrease moving distally along the dental arcade of one individual, reflecting eruption patterns.

Ten permanent molars (DNH 7, 8, 27, 14, 3, 18/19, & 40) and nine deciduous molars (DNH 44, 96, 60, 107, 108, 30, & 121), making up fourteen *P. robustus* individuals, were chosen for this formative study. This sample consisted of six M1s, two M2s, two M3s, five dm1s, and four dm2s (Table 19). Selection of these specimens was based on the following criteria: varying dentine exposures on the occlusal surface due to non-pathological attrition and complete preservation of the occlusal surface. Of these, three have been assigned histological ages at death (DNH 44, 107, & 108; Smith et al., 2015). It must be noted that one permanent element selected (DNH 14) did not fully meet the set criteria. A small enamel flake is missing on the lingual edge of the hypocone. Enamel at this location is worn thin due to attrition and the outline was estimated across this small gap. The specimen was included despite not meeting the criteria to provide the permanent dental sample with a second M2.

Specimen	Element(s) Used
Permanent	
DNH 3	M^2
DNH 7	RM^1, LM^1, M_1
DNH 8	M_1
DNH 14	M^1
DNH 18/19	M_2, M_3
DNH 27	M_1
DNH 40	M^3
Deciduous	
DNH 30	dm^2
DNH 44	dm_1
DNH 60	dm_1, dm_2
DNH 96	dm_1
DNH 107	dm_1, Ldm_2
DNH 108	Ldm^1
DNH 121	dm^2

Table 19: Specimens and elements used in dental wear study; Left and right only specified when antimerical elements were assessed.

6.2 Results

Results are presented in Figures 17-26. When compared to the previously presented relative age seriation, the hypothesis that a greater percentage of wear would be recorded from older individuals was supported in all but three specimens (DNH 27, 96, & 107). In the three instances where different elements from one individual could be examined, the hypothesis that the percentage of wear will decrease moving distally along the dental arcade of one individual was supported. Assessment of three M1s from DNH 7 also allowed for assessment of intra-individual variation, both left to right and maxillary to mandibular. Assessment of three individuals with chronological age allowed for a preliminary interpretation of rate of wear from age 1.7 to 5.35/5.53 years.

6.2.1 Permanent Dentition

While the M2 and M3 comparisons (Figures 18 & 19) supported the hypothesis that a greater percentage of wear would be recorded from older individuals, the M1 comparison (Figure 20) did not. In this assessment DNH 27 was shown to be at an equivalent state of wear to DNH 8 and a lesser state of wear than DNH 7 despite being placed as older than DNH 7 in the previously presented relative age seriation. If this methodology is accurate, the placement of DNH 27 in the seriation is incorrect and this specimen instead belongs at an equivalent age to DNH 8. The minimal disparity seen between DNH 8 and DNH 27 (0.283%) can easily be accepted as individual variation. The hypothesis that the percentage of wear would decrease distally down the dental row to reflect formation patterns is clearly supported by DNH 18/19 (Figure 21).
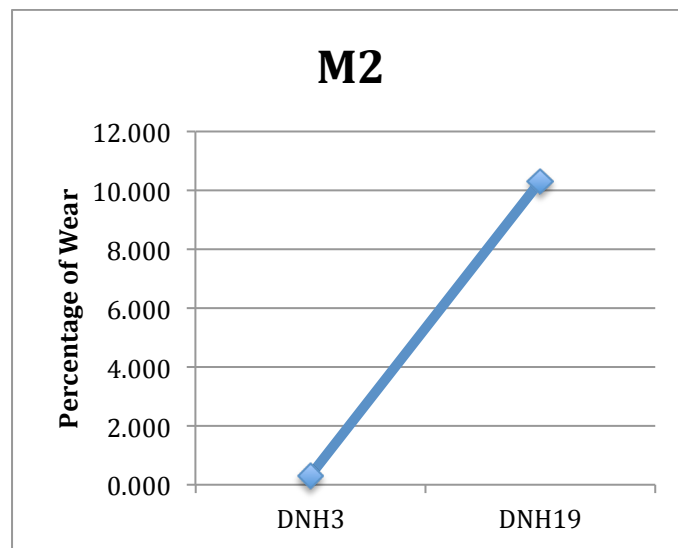
Figure 18: M2 wear assessment

Figure 19: M3 wear assessment
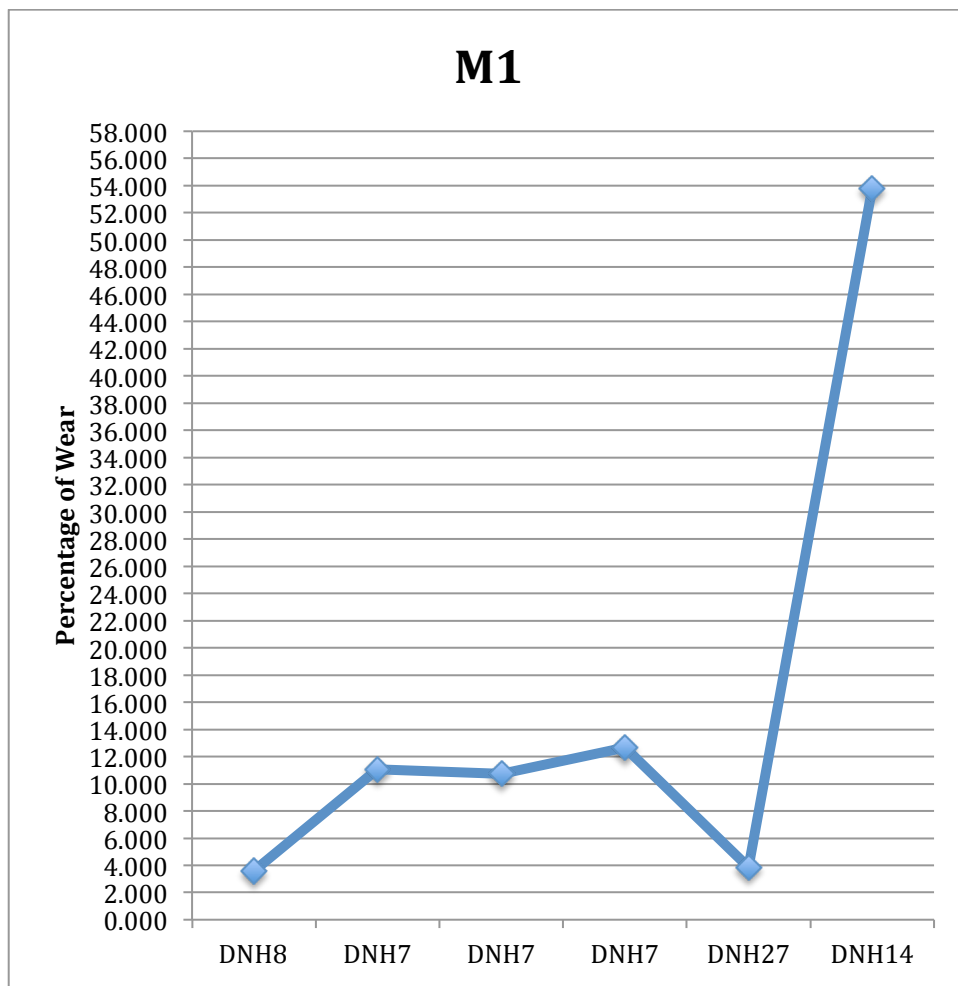
Figure 20: M1 wear assessment
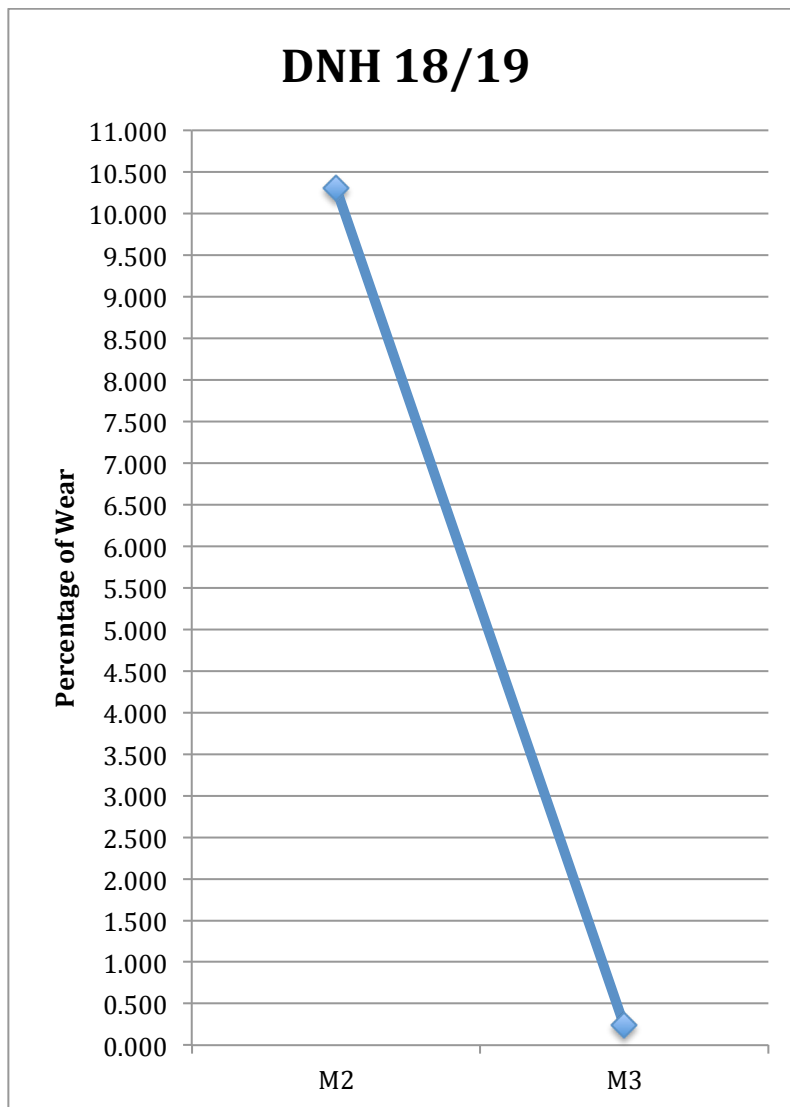
Figure 21: DNH 18/19 wear assessment

Intra-individual variation is exhibited in the assessment of DNH 7 (Figure 22). The upper antimerical elements exhibit very similar wear (11.078% and 10.713%; difference of 0.365%) while the lower element shows a greater disparity when compared with the upper elements (12.683%). While this only represents a difference of 1.605 - 1.970%, this may indicate a slight variation in the eruption timing of maxillary versus mandibular dentition. However, a larger sample size would be required to determine if this is the case or if the disparity is simply due to individual variation.
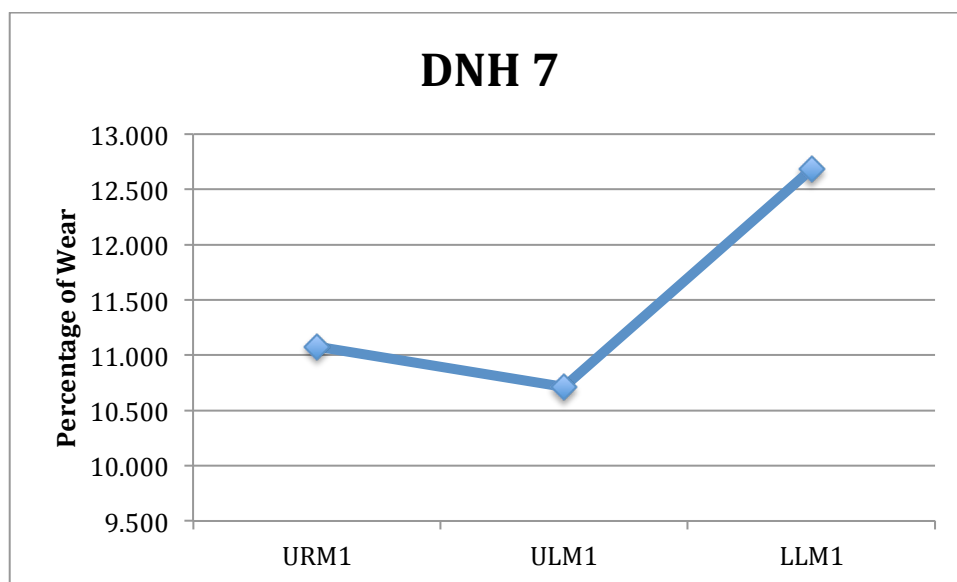
Figure 22: DNH 7 wear assessment

6.2.2 Deciduous Dentition

While the dm2 comparison (Figure 23) supported the hypothesis that a greater percentage of wear would be recorded from older individuals, the dm1 comparison (Figure 24) did not. This may indicate the DNH 96 and DNH 107 have been placed incorrectly in the relative age seriation, as is possible with DNH 27, and instead represents a younger specimen than first suspected. Assessment of DNH 44 however suggests an atypical formation and eruption rate that may instead cause the specimen to show a percentage wear that is inconsistent with its attributed age (as discussed in Chapter 4; Figure 11). DNH 44 was aged at 1.7 years through histological methods (Smith et al. 2015). The states of wear exhibited on the elements in occlusion however, seem inconsistent to the stage of formation and eruption of the non-occluding elements when compared to other individuals within the Drimolen assemblage. As histological aging relies on the assumption that the M1 begins formation at or around the time of birth (Smith et al. 2015), it is possible that if this rate was atypical and did not reflect this assumption, the assigned histological age could be inaccurate. It is likely that this atypical pattern in DNH 44 is convoluting the results of the dm1 comparison as a disparity of only 3.121% between DNH 44 and DNH 107 is recorded despite the former having been assigned a chronological age of 1.7 years and the latter a chronological age of 4.82 years by Smith et

al. (2015). The hypothesis that the percentage of wear would decrease distally down the dental row to reflect formation patterns is clearly exhibited in DNH 60 and DNH 107 (Figures 25 & 26).
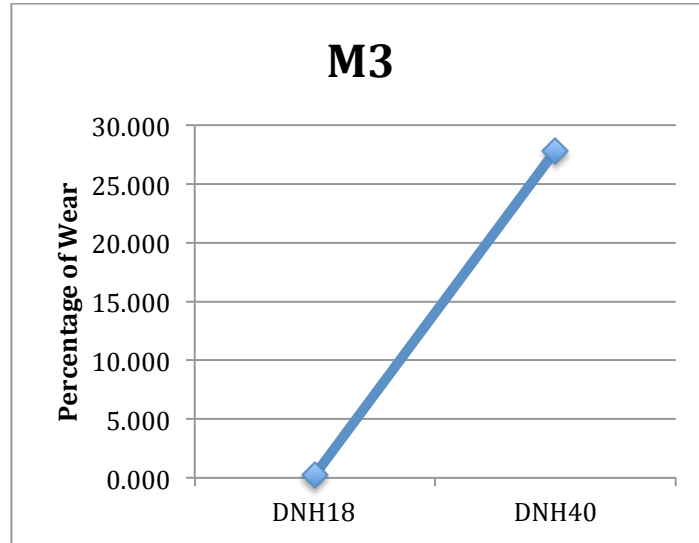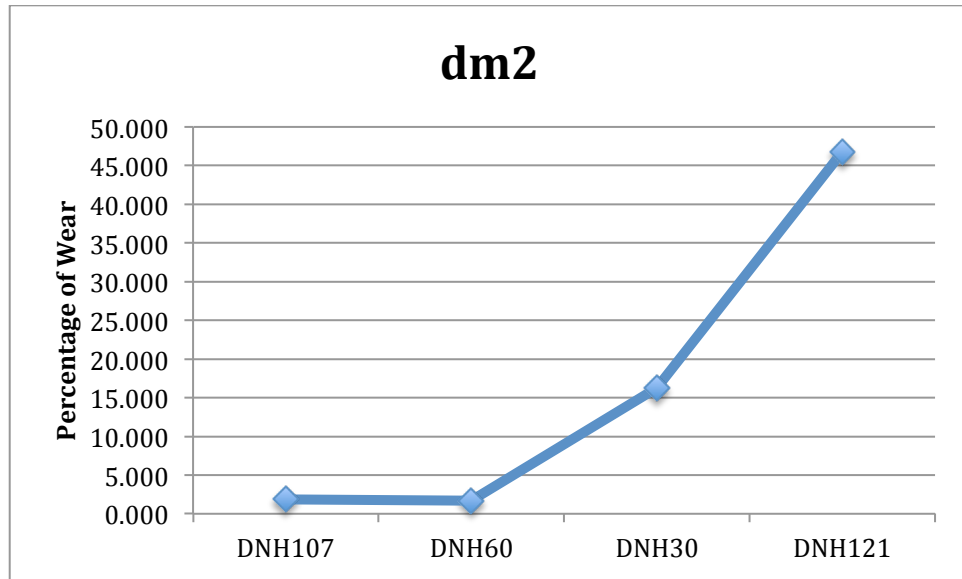

Figure 23: dm2 wear assessment
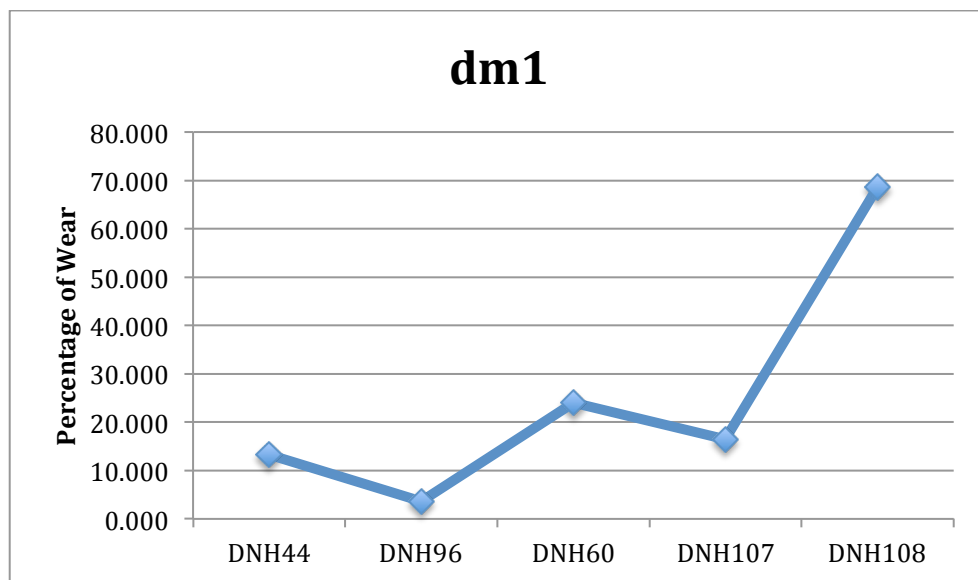
Figure 24: dm1 wear assessment
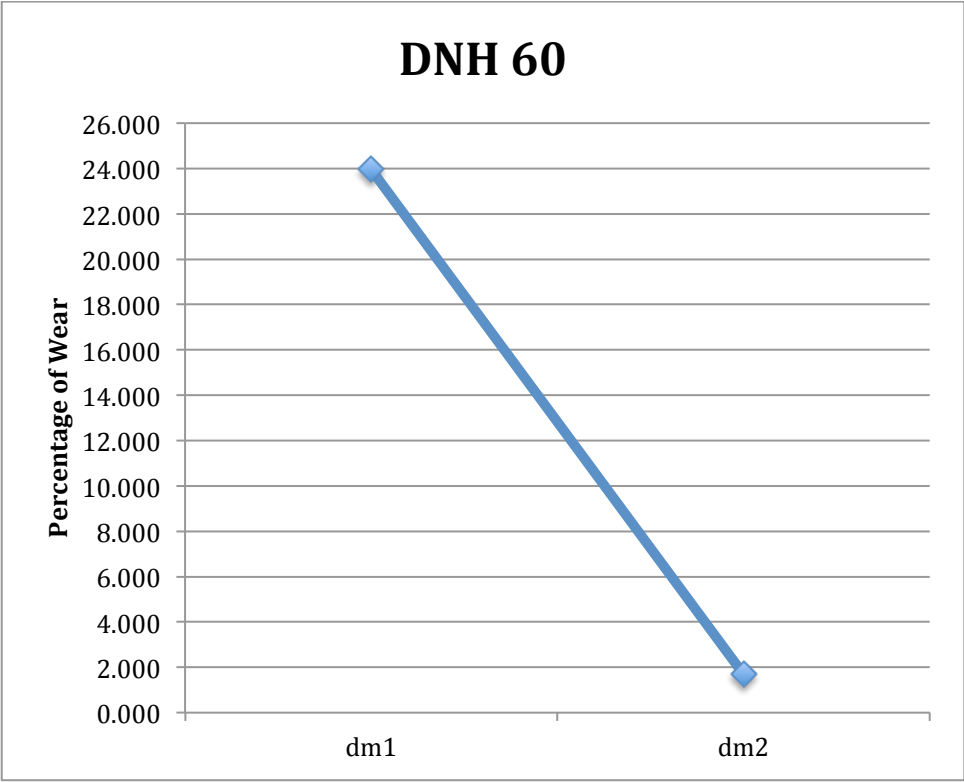
Figure 25: DNH 60 wear assessment
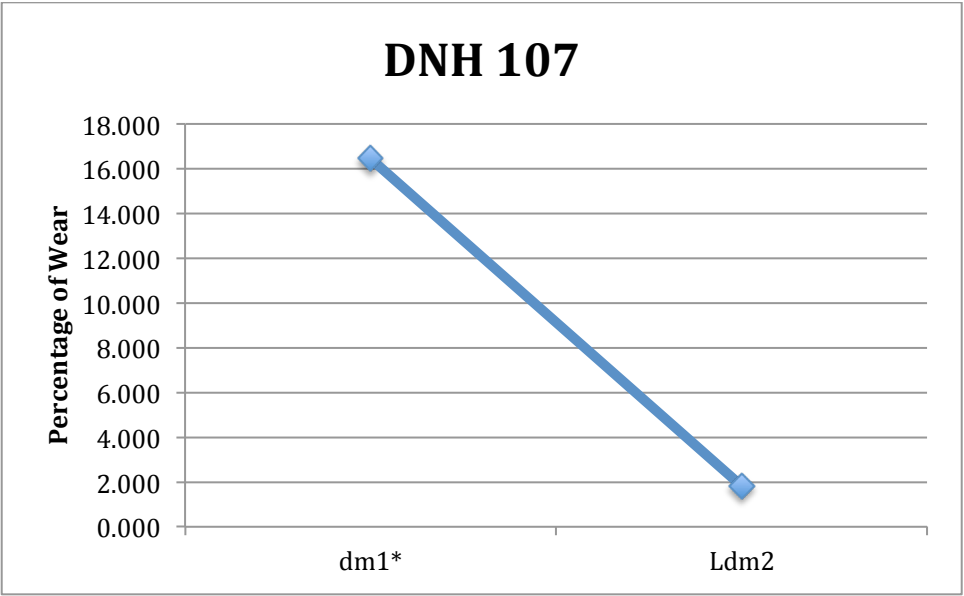
Figure 26: DNH 107 wear assessment

6.2.3 Aged Specimens

A comparison of the percentage of wear of dm1s belonging to specimens with chronological ages was examined for the purposes of preliminarily assessing rate of wear (Figure 27). Three specimens aged at 1.7 years (DNH 44), 4.82 years (DNH 107), and 5.35/5.53 years (DNH 108) by Smith et al. (2015) were assessed. This comparison yielded an unexpected result. As mentioned above, despite an age difference of 3.12 years, DNH 44 and DNH 107 display a wear disparity of only 3.121%. On the other hand DNH 107 and DNH 108, display a wear disparity of 52.153% despite an age difference of only 0.53/0.71 years. This indicates a 3.121% increase over 3.12 years and a 52.153% increase over 6.36/8.52 months. While the disparity in percentage of wear between DNH 44 and DNH 107 may be artificially small due to the potential of atypical eruption discussed above, a significant increase after the age of 4.82 years is still evident. That is, even if the dm1 of DNH 44 exhibited 0% dentine exposure (unlikely as DNH 47 aged at 0.67-0.77 years already exhibits enamel faceting), only an increase of 16.461% would be recorded over 3.12 years.
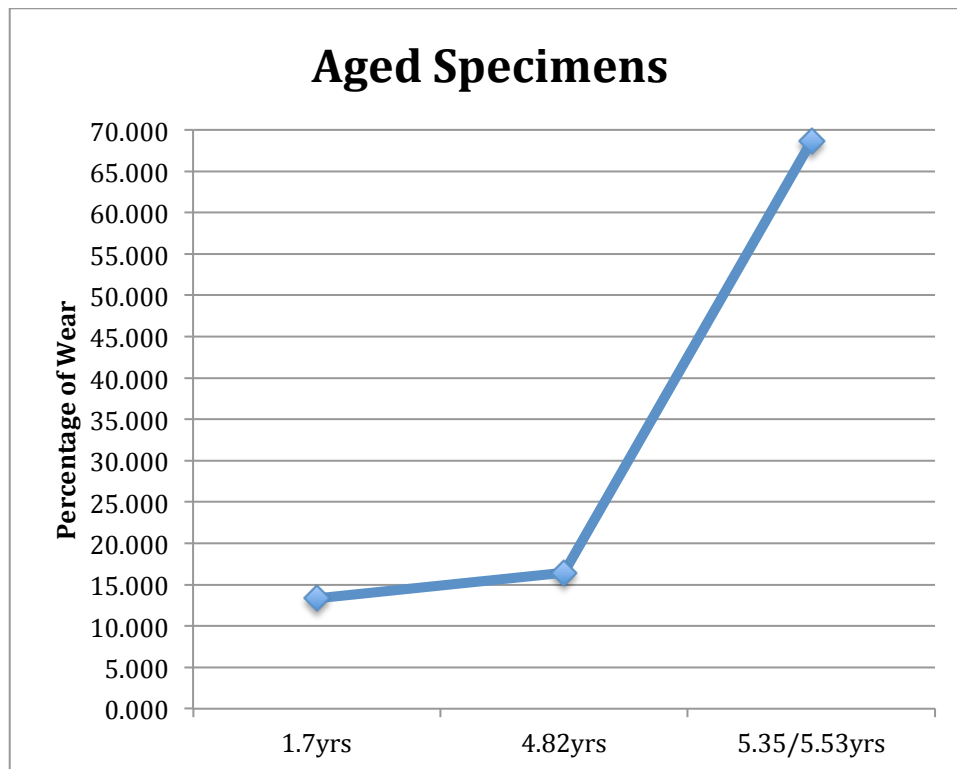
Figure 27: Aged specimens wear assessment

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While it is possible that this apparently rapid increase in percentage of wear is due in part to individual variation, this phenomenon potentially displays a significant marker in *P. robustus* life-history. This analysis shows a shift from 0.083% per month to 8.200/6.121% per month at approximately 4.82 years of age. DNH 107 and DNH 108 both fall within the Mixed Dentition category (Chapter 4). The former individual shows a newly erupted M1 with the dm1 and dm2 not yet shed. All other permanent dentition excluding the M3 are not yet erupted, exhibiting varied states of formation. 6.36/8.52 months later, the latter individual shows the M1, I1 and C in wear, with the dm1 and dm2 still in the mouth. All other permanent dentition excluding the M3 are not yet erupted, exhibiting varied states of formation. Further study would be required to determine if this significant increase in rate of wear is indicative of weaning age or age of solid food transition. However, the position of these individuals in the early to mid-Mixed Dentition category is more suggestive of a solid food transition as individuals exhibiting this eruption stage would most probably have already been weaned.

7. Demographic Interpretation

7.1 Introduction

Demographic profiles are an important tool for interpreting assemblage as they can provide both pre- and peri-depositional taphonomic data, as well as bio-behavioural data of the species in question. Non-anthropogenic accumulation processes, such as fluvial aggregation, carnivore denning, and death trap deposits, as well as autochthonous accumulations, such as living sites where the individuals represented entered the site alive and were deposited in the context in which they fossilised, can potentially be distinguished through examination of age profiles. While age profiles must be considered concurrently with taphonomic and geological data to interpret depositional processes and potential bias, demographic profiles represent a key piece of such an investigation. Methodologies such as those proposed in the preceding chapters will continue to elucidate species-specific characteristics necessary for the interpretation of life-history characteristics such as life-expectancy, length of childhood and other factors regarding group behaviours.

7.2 Methods

7.2.1 Comparative Populations

Four demographic datasets (extant baboons, extant chimpanzees, fossil Drimolen baboons, fossil Swartkrans Member 1 *P.*) were analysed against both the Drimolen *P. robustus* and Drimolen *Homo* assemblages:

1. Wild Chimpanzees: The first population consists of five groups of wild chimpanzees from Nigeria, Côte d'Ivoire, Uganda, Tanzania, and Guinea documented in a longitudinal study and presented by Hill et al. (2001). The demography of this population represents a natural attrition profile (Hill et al. 2001).

2. Wild Baboons (*Papio ursinus*): The second population consists of a troupe of wild baboons from Botswana observed over a 30-month period by Busse (1980). The demography of this population represents a leopard predation profile (Busse 1980).

3. Drimolen Fossil baboons (*Papio hamadryas robinsoni*): The third population consists of the Drimolen baboon assemblage adapted from Nieuwoudt (2015). This population has been suggested to represent a living population deposited due to cave utilisation as well as a carnivore accumulation (Nieuwoudt, 2015). That is, Nieuwoudt (2015) suggested this assemblage represented two separate phases of deposition: a natural, living site accumulation and a carnivore accumulation. Though this demography is not drawn from a living, observable population, it has been treated as such for the purposes of this study. As with the Drimolen *P. robustus* assemblage, site stratigraphy and context of the fossil remains suggest a relatively rapid deposition and an apparent lack of spatially isolated specimens (Mallett 2015; Herries et al. in prep); as such this assemblage is treated in this thesis as a palaeo-population.

4. The fourth population consists of the Swartkrans Member 1 *P. robustus* assemblage deriving from Member 1 Hanging Remanent (between 1.96-1.80 Ma; Herries & Adams 2013). The MNI presented by Mann (1975) was utilised for the interpretation of this assemblage to maintain consistency with previous analyses presented here. Again, this demography is not drawn from a living population but will be treated as such for the purposes of this study. It is accepted that this assemblage represents a carnivore accumulation and has been treated as a population previously (Vrba 1976; Brain, 1981; 1993) For the purposes of this study, the Swartkrans Member 1 *P. robustus* assemblage will be treated as a palaeo-population due to both these previous arguments and contextual data discussed previously (Chapter 2).

Each of these groups was treated as a biological or palaeo-population, defined as a contemporaneously living group. The Kromdraai B *P. robustus* assemblage was not included as Mann (1975) identified only four individuals.

7.2.2 Methods
The six groups were placed into one of five categories:

- No dentition in occlusion

- Deciduous dentition only

- Mixed dentition

- Permanent dentition only (prime-age)

- Old adult

The first four categories were defined solely on the dental elements in occlusion. Fossil hominin palaeo-populations were attributed based on visual inspection while the extant populations were attributed based on known eruption times (Nissen and Riesen 1964; Smith et al. 1994). The fossil baboon assemblage was assigned to categories based on reported dental elements in occlusion by Nieuwoudt (2015; Appendix 5). The fifth category was defined based on life expectancy. In the three hominin assemblages, individuals were placed in the "Old Adult" category when the state of wear was extremely advanced indicating the individual could not have continued to survive for a significant amount of time (i.e. DNH 17; Figure 28). The number of individuals in each category was then calculated against the total population to determine the proportion of the population represented. In the case of the extant populations, the number of individuals in each category was calculated against the total number of dead individuals. As fossil assemblages represent only the deceased portion of the population, individuals still alive in the extant populations at the end of the period of study could not be included without artificially altering how the categories reflected the population. As highly accurate ages at death (± 2 months) cannot be determined and the life-history of *P. robustus* and early *Homo* is largely unknown (Lyman 1994), comparisons made here have been limited to these five categories representing un-equal times. That is, one category may represent three years and another 15, as the categories are defined on dental stages as opposed to the exact ages of the individuals.

Figure 28: DNH 17

A series of χ^2 tests of independence were applied using PAST 3.10 (Hammer et al. 2001) between compared demographic profiles. This test relies on two main assumptions: the independence assumption and the sample size assumption. The former assumption is satisfied by the dataset tested here as the two variables (population and dental stage) are not correlated data. The latter assumption is violated in some instances as not all demographic profiles tested contain individuals in each dental category. Where appropriate, a secondary χ^2 test was run excluding dental categories that do not overlap in the populations being compared (e.g. one or both populations have zero individuals in a particular dental category). However, due to the nature of fossil assemblages, these decisions were made on a case-by-case basis (detailed below). The Alpha level (significance value) was set at 0.05. The null hypothesis states that the populations tested are the same. That is, both populations represent the same demographic profile and so similar accumulation processes.

7.3 Results

7.3.1 Individual Demographic Profiles

7.3.1.1 Drimolen P. robustus (Figure 29)

The best represented category in the Drimolen *P. robustus* palaeo-population is the Permanent Only category at 50% of the total population. The Mixed Dentition category (21%) is the next best represented followed by the Deciduous Only category (19%), Old Adult category (8%), and No Dentition in Occlusion category (1%). As a whole, 42% of the population is below prime age.
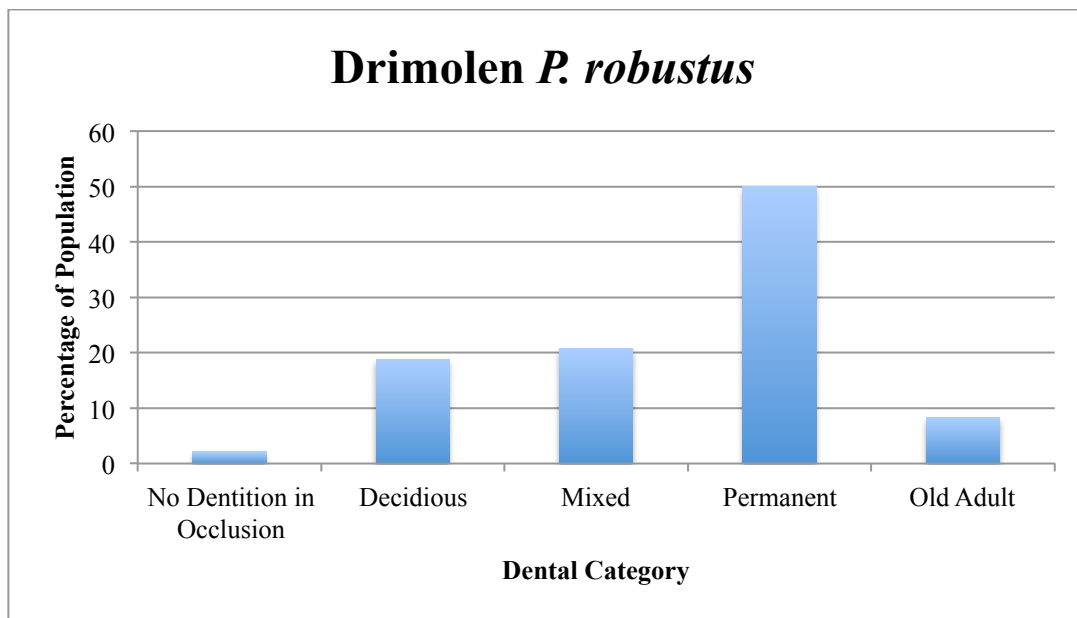
Figure 29: Demography profile of Drimolen P. robustus.

7.3.1.2 Drimolen Homo (Figure 30)

The best represented category in the Drimolen *Homo* palaeo-population is the Deciduous Only category at 78% of the total population. The Mixed Dentition and Permanent Only categories are the next best represented, each at 11% of the total population. The Old Adult and No Dentition in Occlusion categories are not represented within this population. As a whole, 89% of this population is below prime age.
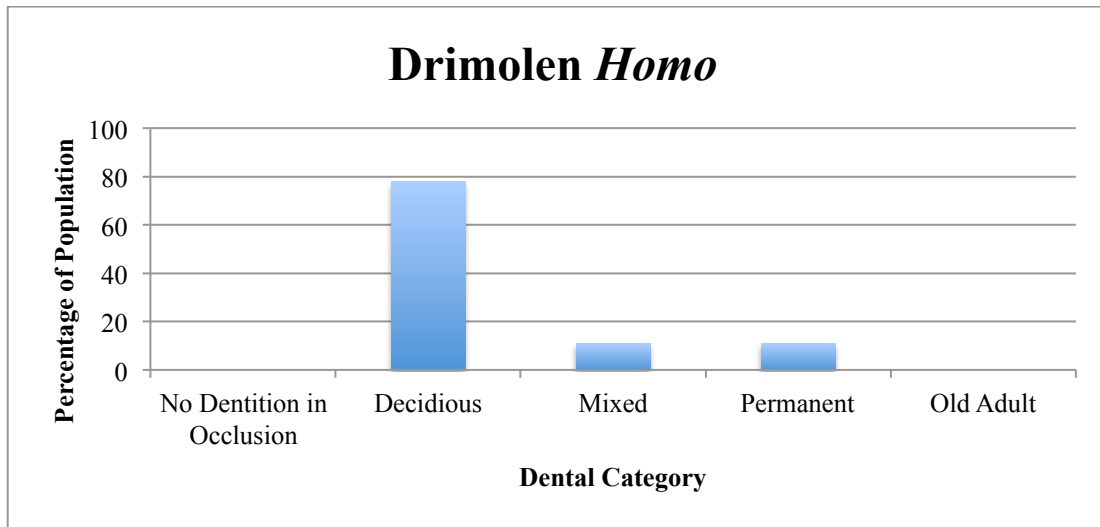
Figure 30: Demography profile of Drimolen Homo.

7.3.1.3 Chimpanzee (Figure 31)

The demography of the wild chimpanzee population representing a natural attrition pattern also shows the Permanent Only category as the best represented at 31%. The next best represented category is the No Dentition in Occlusion category (21%), followed by the Mixed Dentition category (20%), Deciduous Only category (19%), and Old Adult category (8%). As a whole, 60% of the population is below prime age.
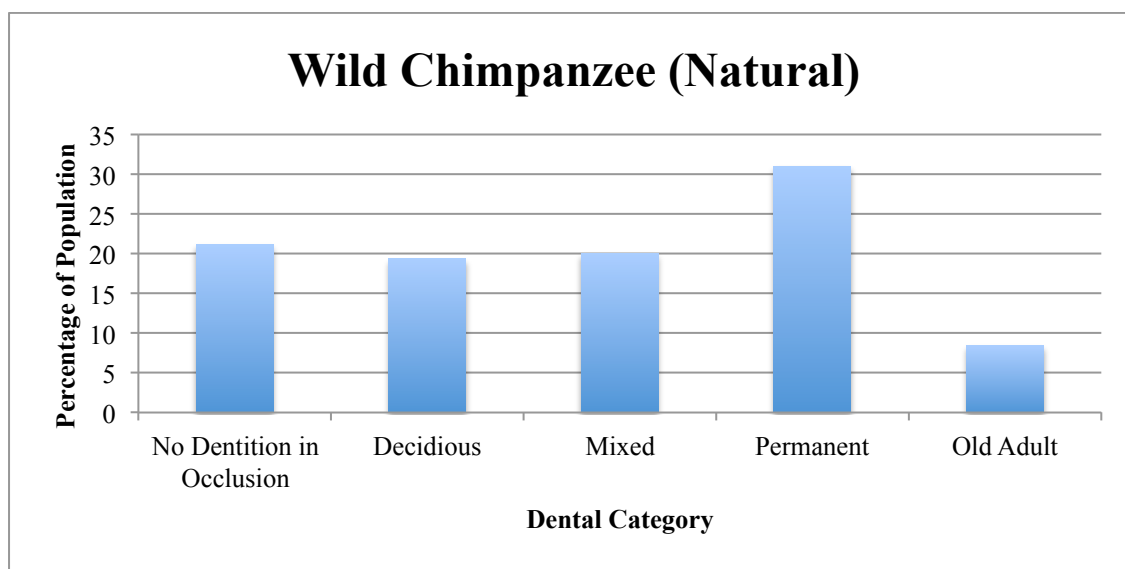
Figure 31: Demography profile of wild chimpanzee (natural)

7.3.1.4 Baboon (Figures 31 & 32)

Extant Baboon

The wild baboon population representing a predation profile only consists of individuals in the Mixed Dentition and Permanent Only categories. Again, the Permanent Only category is the best represented at 87.5%. The Mixed Dentition category represents 12.5%. As a whole, 12.5% of the population is below prime age.
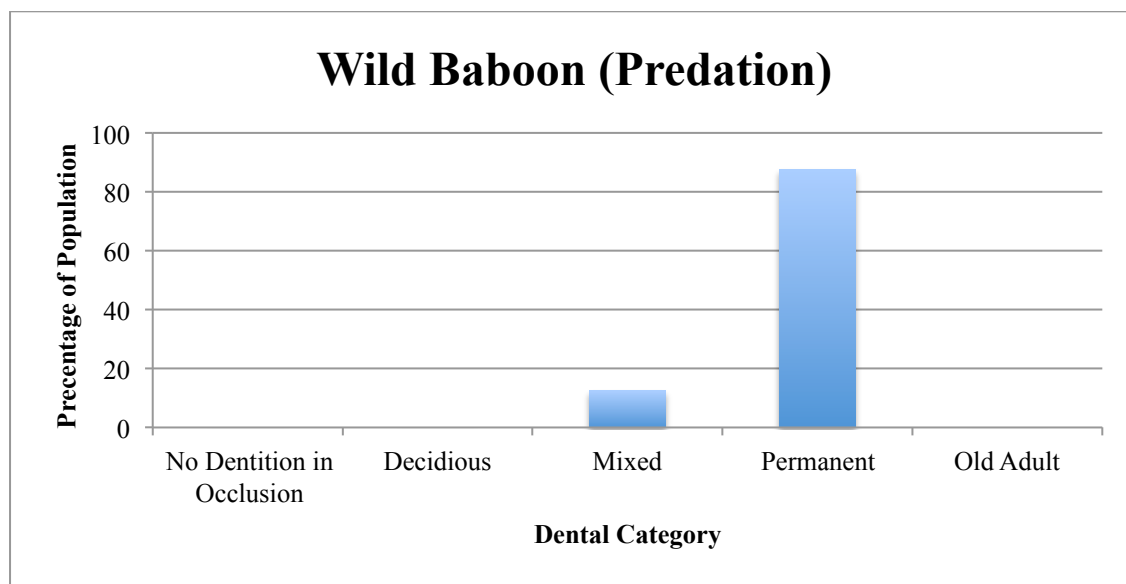
Figure 32: Demography profile of wild baboon (predation)

Drimolen Baboon

The demography of the Drimolen baboon fossil assemblage shows the Permanent Only as the best represented category at 46%. The next best represented is the Old Adult category (21%), followed by the Deciduous Only category (14%), the Mixed Dentition category (11%), and the No Dentition in Occlusion Category (9%). As a whole, 34% of the population is below prime age.
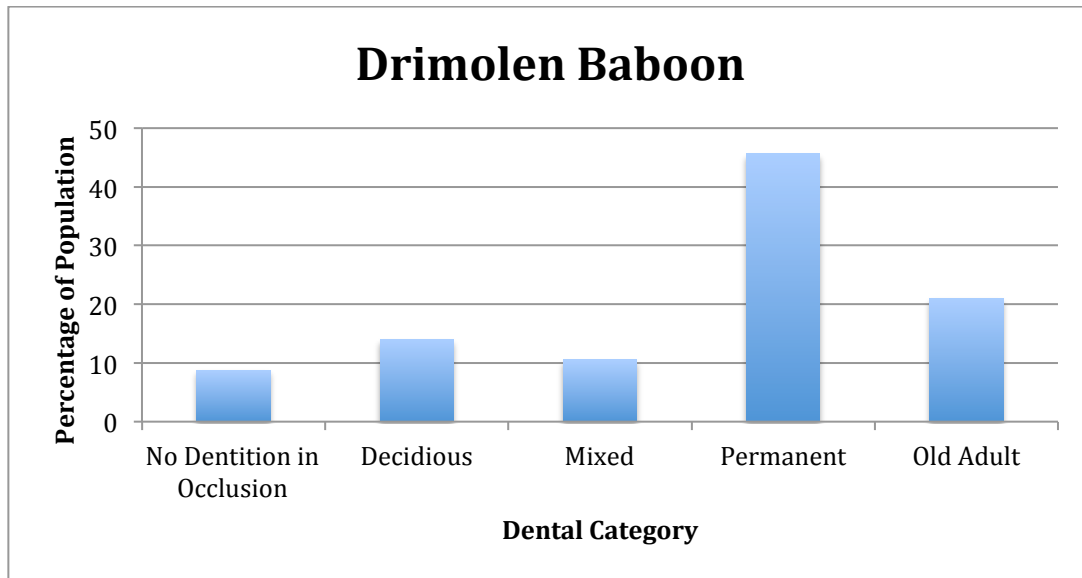
Figure 33: Demography profile of Drimolen baboon

7.3.1.5 Swartkrans Member 1 P. robustus (Figure 34)

The demography of the Swartkrans Member 1 *P. robustus*, thought to represent a carnivore accumulation, again shows the Permanent Only category as the best represented at 78% of the population. The Mixed Dentition category is the next best represented at 22% followed by the Deciduous Only category at 8%. Neither the No Dentition in Occlusion nor the Old Adult categories are represented in this assemblage. As a whole, 30% of the population is below prime age.
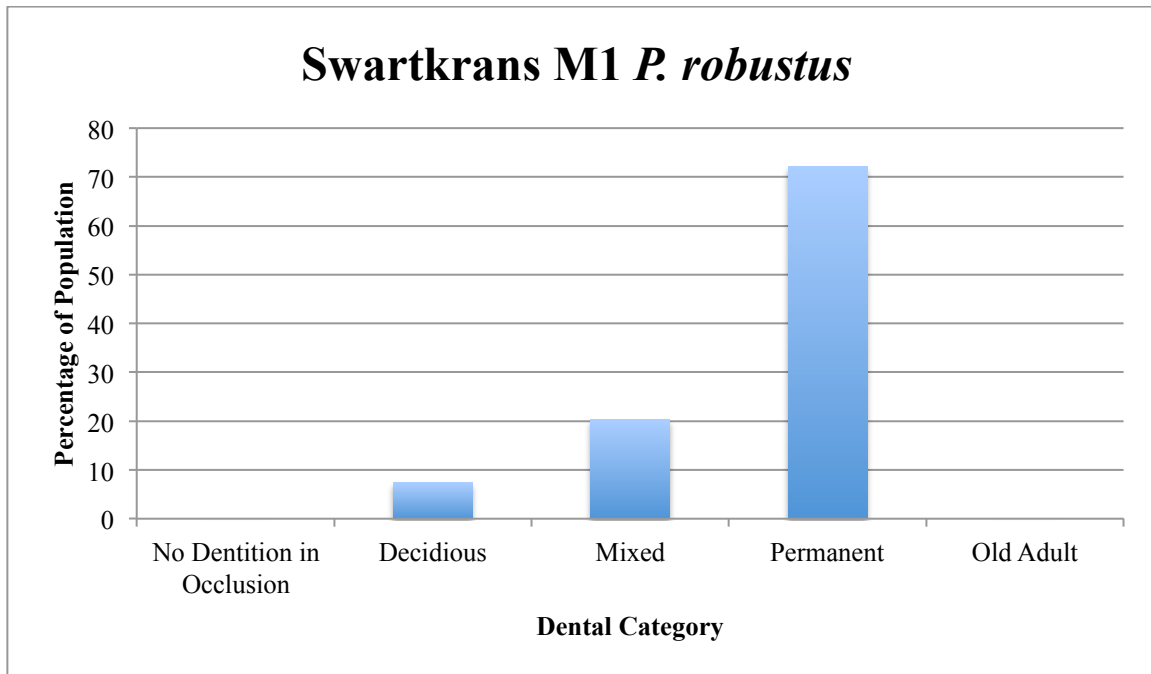
Figure 34: Demography profile of Swartkrans M1 P. robustus

7.3.2 Demographic Comparisons

Demographic comparisons are presented in Tables 35-43.

7.3.2.1 Drimolen P. robustus

Of the five populations, the demographic profile of the Drimolen *P. robustus* is most similar to that of the extant baboon predation profile (Figure 35). This baboon demography includes individuals only within the Mixed Dentition and Permanent Only categories but, again, is similar when relative representation is examined. Two χ^2 tests were run between these two populations. The first included all five categories, inclusive of the three categories within the extant baboon assemblage that do not contain any individuals. This test yielded a p-value of 0.36. The second test excluded categories that did not contain individuals in both populations and instead compared only the Mixed Dentition and Permanent Only categories. This approach however, excluded 29% of the Drimolen *P. robustus*. Despite this issue, the limited χ^2 test yielded a p-value of 0.33— similar to that of the inclusive test. Both versions of the χ^2 test assessing the independence of the Drimolen *P. robustus* population and the extant baboon (predator

accumulation) yielded results that support the null hypothesis that these populations represent the same demographic profile.
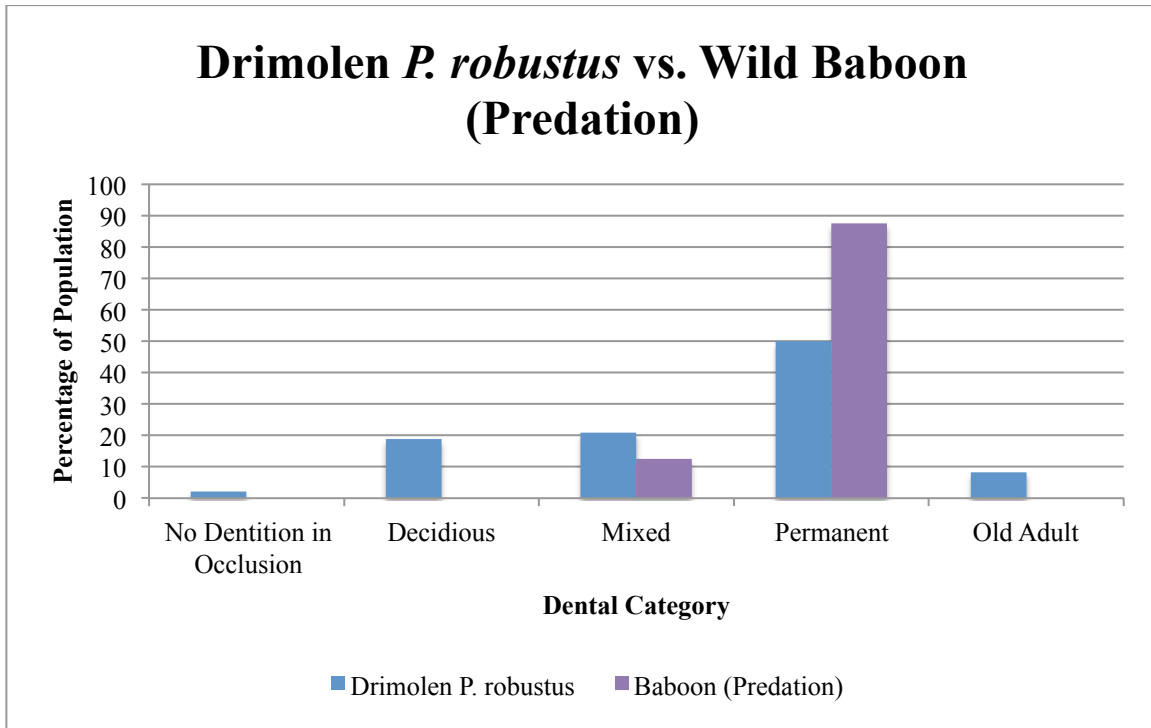
Figure 35: Comparison of the demographic profiles of Drimolen P. robustus *and wild baboon (predation)*

The demography profile of the Drimolen baboon (Figure 36) included individuals attributed to all five age categories. The χ^2 test run between the Drimolen *P. robustus* and the Drimolen fossil baboon (suggested to represent a living site and carnivore combination profile; Nieuwoudt 2015) yielded a p-value of 0.13. While this result is not as strong as that yielded from the extant baboon population, it is in support of the acceptance of the null hypothesis.
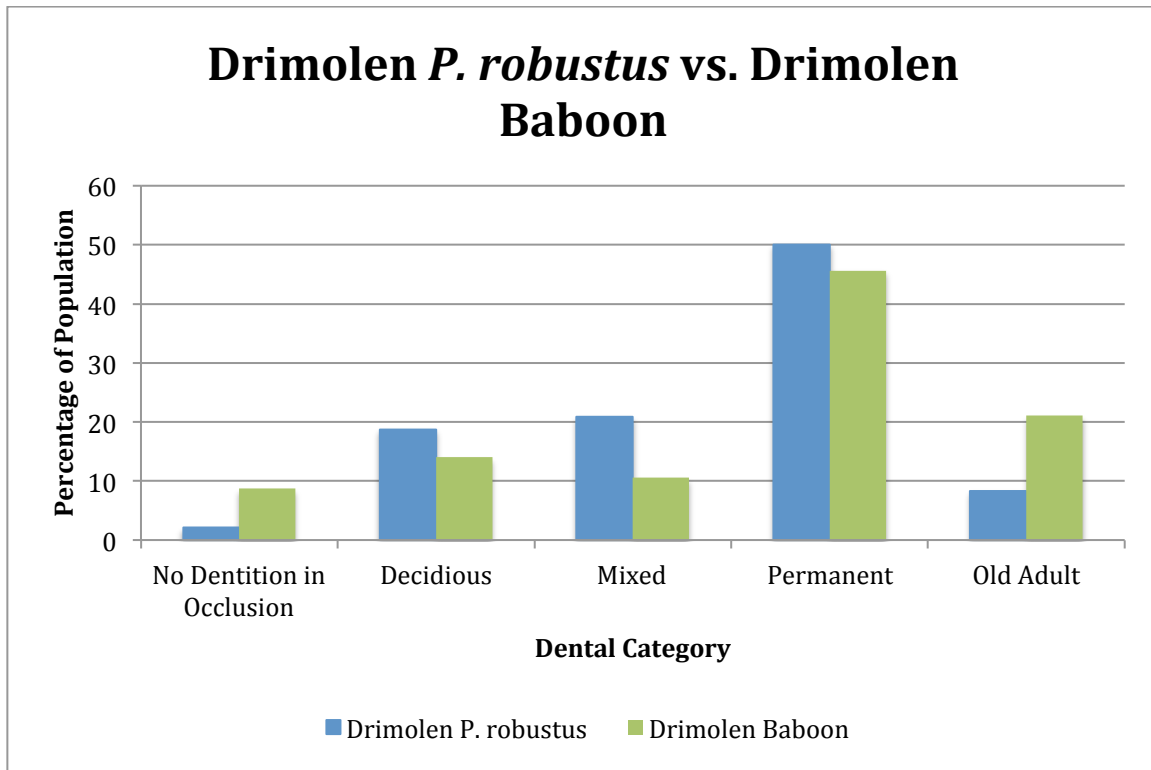
Figure 36: Comparison of the demographic profiles of Drimolen P. robustus *and Drimolen baboon*

While no other comparative populations reached the significance value of 0.05, the Swartkrans Member 1 *P. robustus* profile (Figure 37) was close. As with the extant baboons, two χ^2 tests were run between these populations. The first again included all five categories, inclusive of the No Dentition and Old Adult categories, which lacked individuals within the Swartkrans profile. This test yielded a p-value of 0.001, indicating that the null hypothesis must be rejected. However, the absence of Swartkrans Member 1 *P. robustus* individuals within these two categories may be influenced by sampling bias. As the dentition belonging to individuals within the No Dentition in Occlusion category would likely be found as isolated dental elements, as well as due to their small absolute size, it is reasonable to assume these specimens may not have been collected at Swartkrans do to excavation methodology implemented at the site. In fact, the majority of the Swartkrans Member 1 *P. robustus* material is represented by specimens containing more than one element, supporting the hypothesis that isolated dentition is less likely to have been recovered from this site than from Drimolen. Additionally, the Swartkrans age

data utilised in this demographic analysis is adapted from Mann (1975). Preliminary assessment has lead the author to hypothesis that a reassessment of the Swartkrans Member 1 *P. robustus* material, following the methods presented in this thesis, would result in individuals shifting from the Permanent Only category and into the Old Adult category. Not only would this result in a fourth overlapping category with Drimolen, but it would also remove any artificial inflation from the Permanent Only category. While the latter issue cannot be addressed, a limited χ^2 test was performed inclusive of only the overlapping categories between Drimolen *P. robustus* and Swartkrans Member 1 *P. robustus*. This test yielded a p-value of 0.04. While this value is slightly below the set Alpha level of 0.05, considering the variables detailed above, it is not unreasonable to conclude that this result indicates that the null hypothesis cannot be rejected.
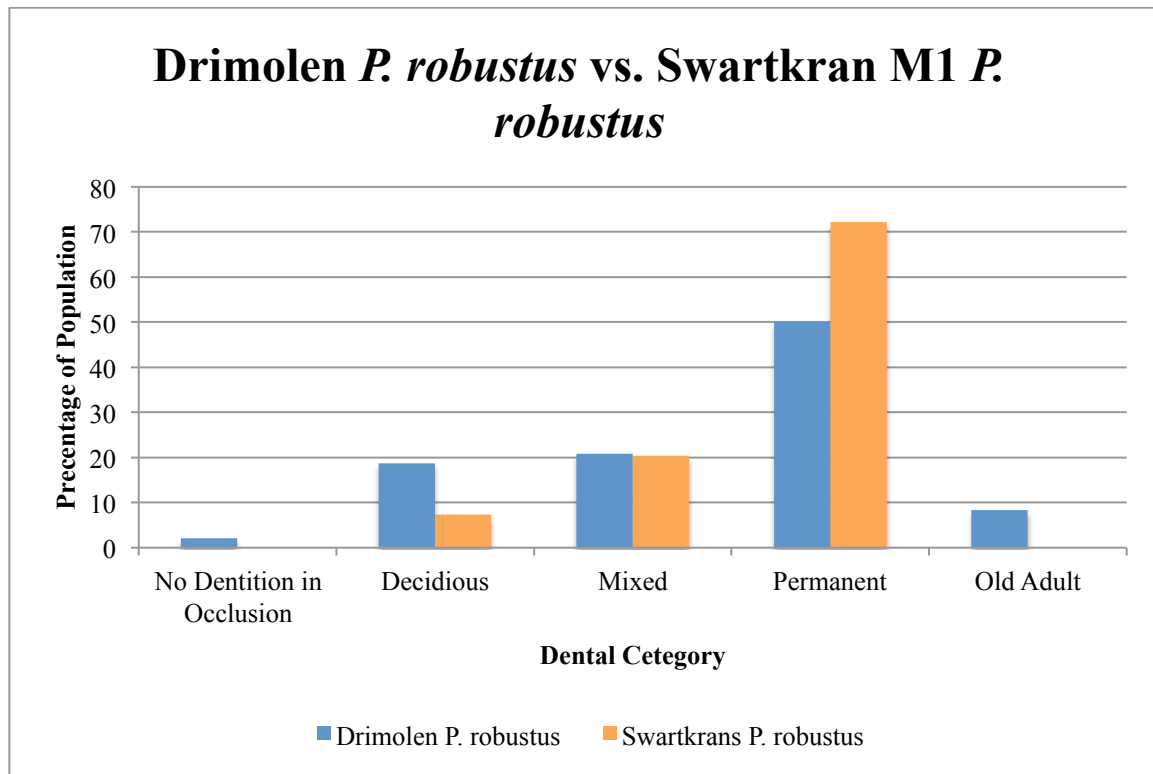
Figure 37: Comparison of the demographic profiles of Drimolen P. robustus *and Swartkrans Member 1* P. robustus

While the extant chimpanzee (Figure 38) demographic profile includes individuals attributed to all five categories, the relative representations of this population is not reflective of the Drimolen *P. robustus* profile. The χ^2 test run between the Drimolen *P.*

robustus and the extant chimpanzee (natural attrition) yielded a p-value of 0.01 and does not support the acceptance of the null hypothesis.
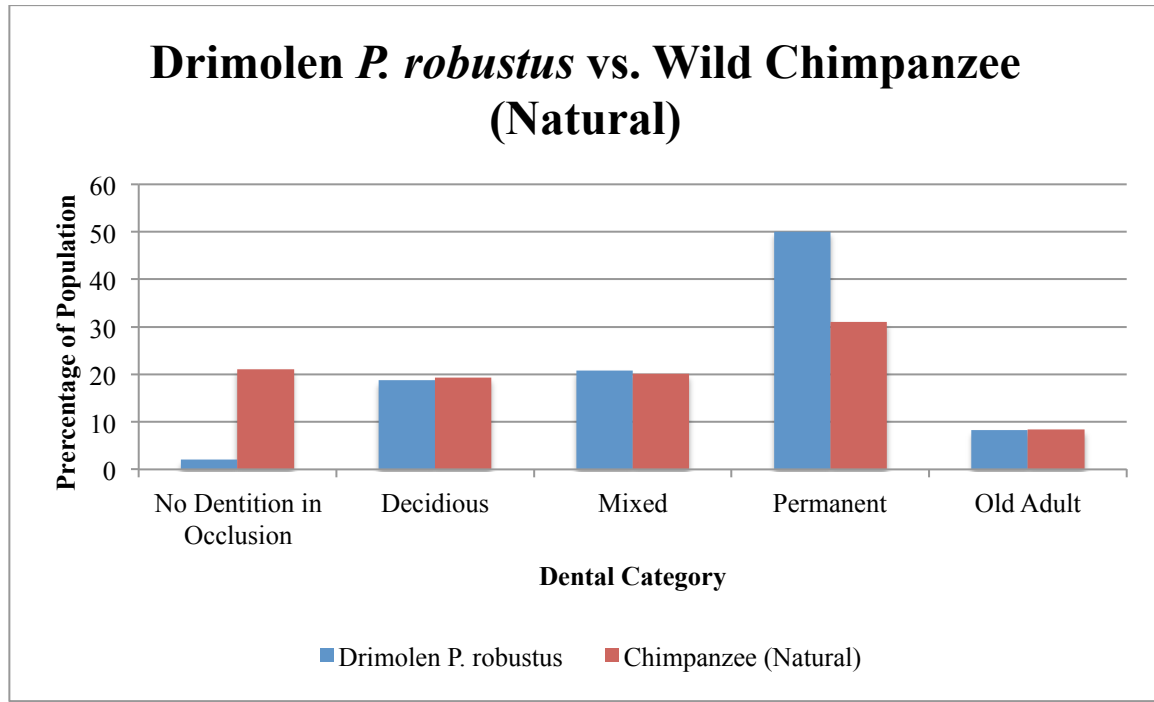
Figure 38: Comparison of the demographic profiles of Drimolen P. robustus *and wild chimpanzee (natural)*

7.3.2.2 *Drimolen* Homo

The demographic profile of the Drimolen *Homo* palaeo-population is dissimilar to that of the Drimolen *P. robustus* palaeo-population, showing instead an apparent inverse profile (Figure 39). Two χ^2 tests were run between these two populations. The first included all five categories, inclusive of the two not represented within the Drimolen *Homo* profile. This test yielded a p-value of 0.009. The second test excluded the No Dentition in Occlusion and Old Adult categories (2% and 8% of the Drimolen *P. robustus* population, respectively). This test yielded a p-value of 0.003. Neither version of the χ^2 test supported acceptance of the null hypothesis.
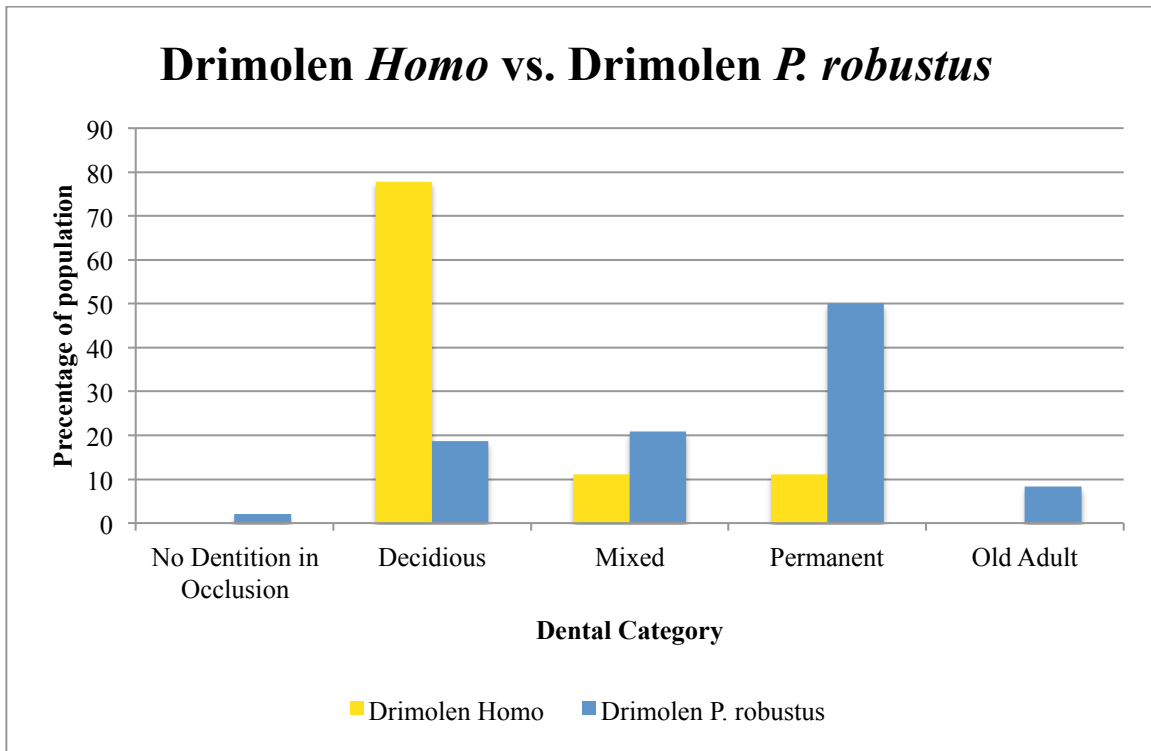
Figure 39: Comparison of the demographic profiles of Drimolen Homo *and Drimolen* P. robustus
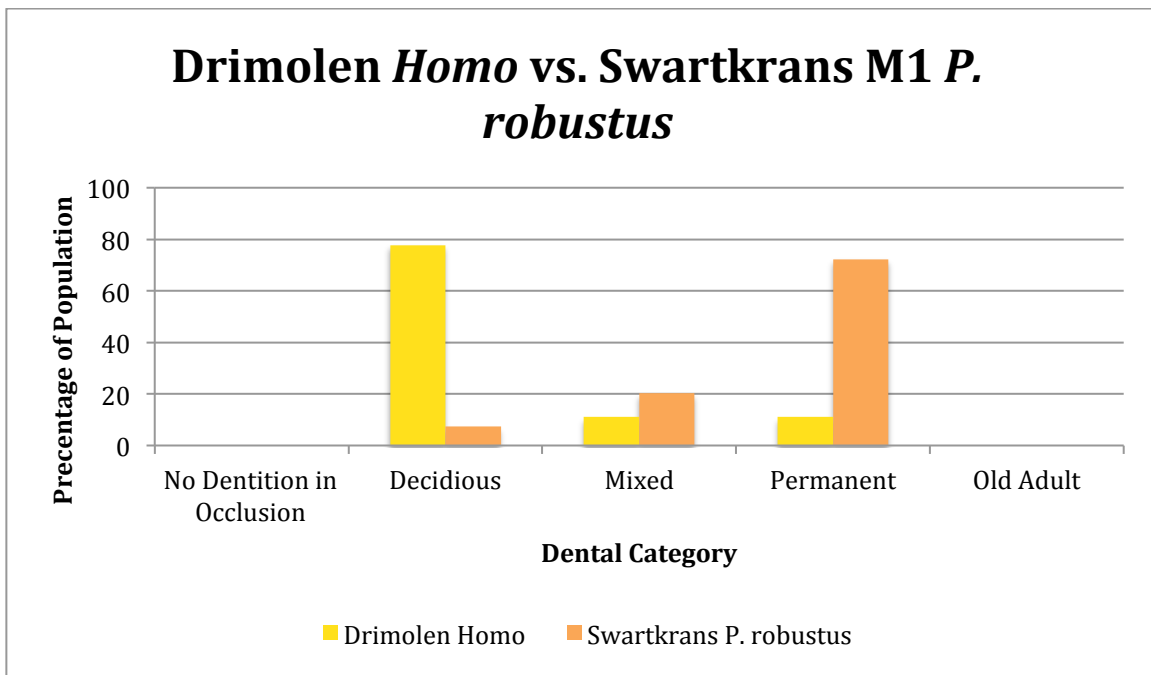
Figure 40: Comparison of the demographic profiles of Drimolen Homo *and Swartkrans Member 1* P. robustus

While the Drimolen *Homo* and the Swartkrans Member 1 *P. robustus* profiles are similar in that the same categories are represented, the relative representation of these categories is again inverse (Figure 40). Two χ^2 tests of these populations were run, again firstly inclusive of all five categories and secondly inclusive only of those categories which overlapped. Both tests yielded a p-value of 9.03E-09, indicating strongly that the null hypothesis cannot be accepted.

χ^2 tests between the Drimolen *Homo* and the Drimolen fossil baboon populations (Figure 41) yielded nearly as strong a result. Two tests were run in the same manner, the first yielding a p-value of 8.43E-4 and the second yielding a p-value of 2.56E-3. Neither of these results support the acceptance of the null hypothesis.
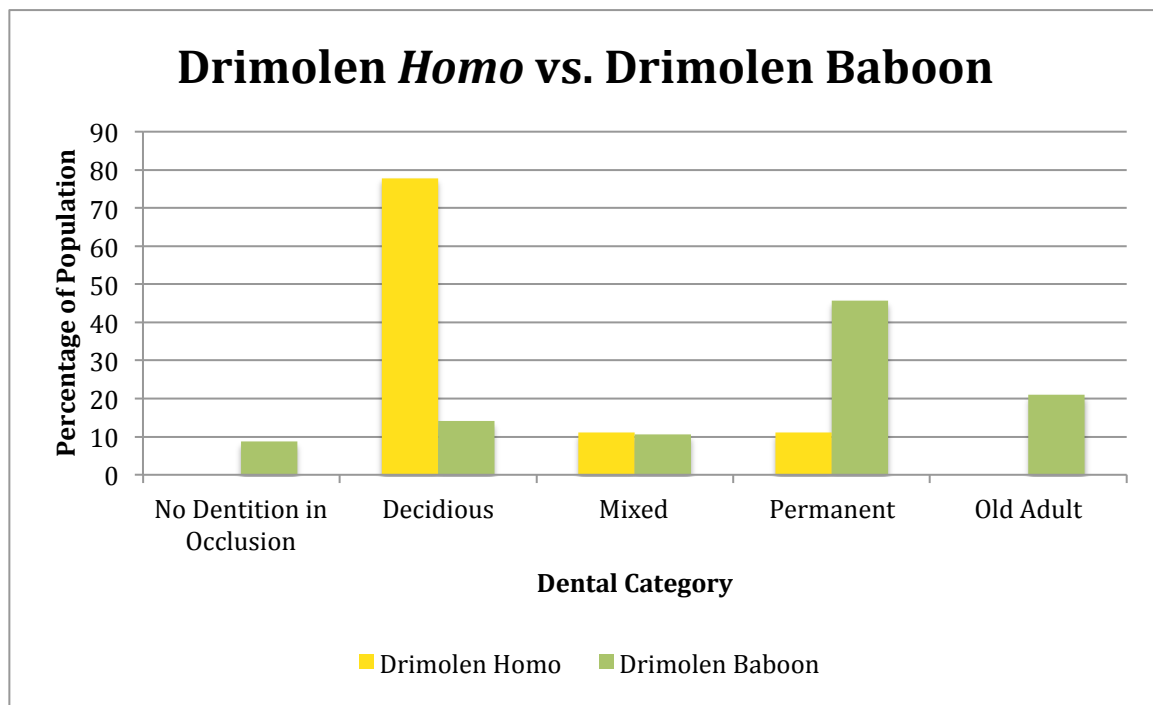
Figure 41: Comparison of the demographic profiles of Drimolen Homo *and Drimolen*
baboon

The demographic profile of the Drimolen *Homo* population as compared to the profile of the extant baboons (predation profile; Figure 42) yielded variable results when assessed

with disparate χ^2 tests. In the case of this comparison, both populations display categories that are not represented. When a χ^2 test is applied only to the two overlapping categories, a p-value of 0.24 is yielded. While this seems in support of the null hypothesis, this result is invalid. The exclusion of the Deciduous Dentition category within the Drimolen *Homo* population for the purposes of eliminating all non-represented categories within the extant baboon population excludes 78% of the Drimolen *Homo* population and reduces the sample size to two. For these reasons, this result has been discarded as erroneous. A χ^2 test inclusive of all five categories and a χ^2 test excluding only the No Dentition and Old Adult categories both yielded a p-value of 0.003 indicating that the null hypothesis cannot be accepted.
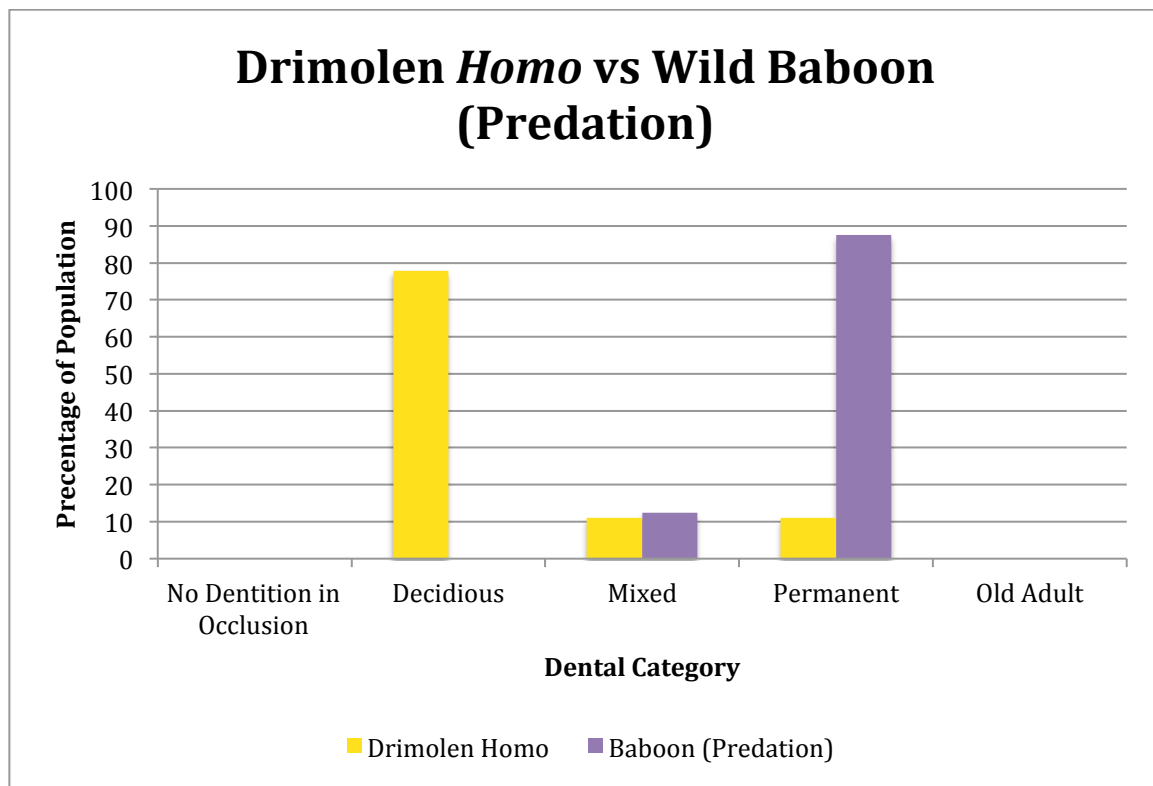
Figure 42: Comparison of the demographic profiles of Drimolen Homo *and wild baboon (predation)*

The *Homo* profile is also dissimilar to the extant chimpanzee population (Figure 43), though the resultant p-values are still well below the significance value of 0.05. A χ^2 test applied to all five categories yielded a p-value of 0.001 and a χ^2 test excluding the two

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categories not represented in the Drimolen *Homo* population yielded a p-value of 0.005. These results are similarly indicative that the null hypothesis cannot be accepted. In the case of the Drimolen *Homo* palaeo-population, a larger sample size would likely clarify these relationships.
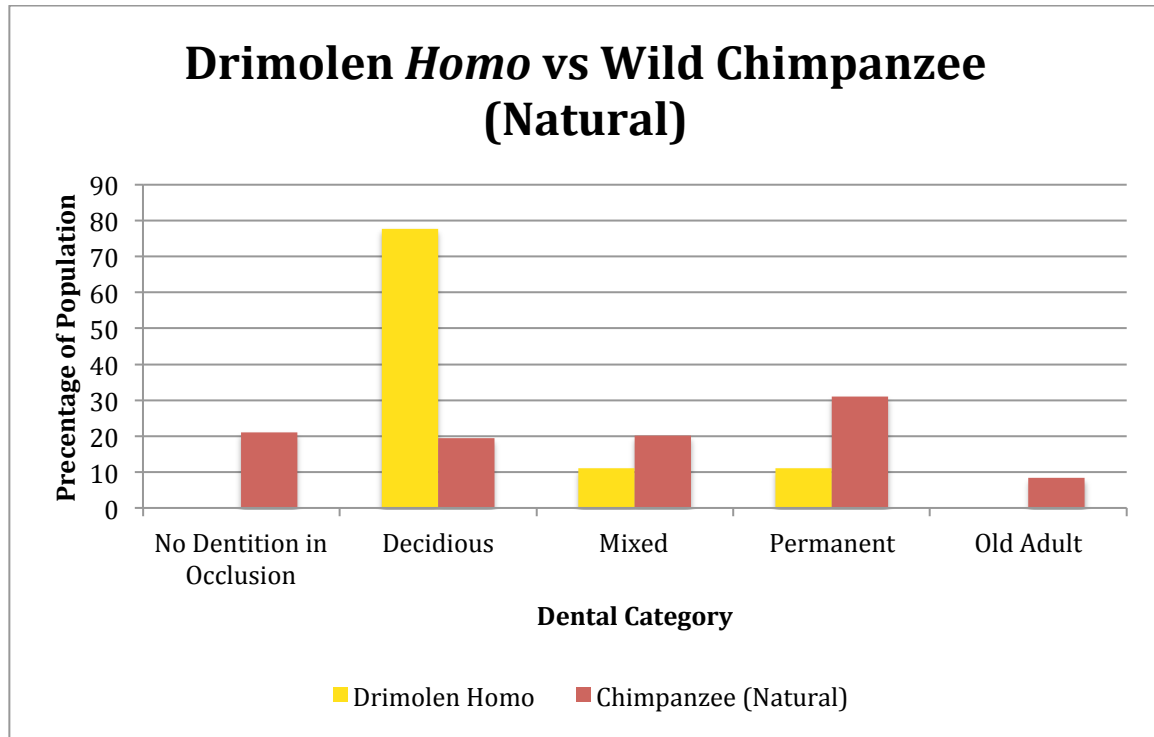
Figure 43: Comparison of the demographic profiles of Drimolen Homo *and wild chimpanzee (natural)*

7.4 Discussion

Mortality curves established from assemblages of skeletal/fossil remains are often described as either attritional (U-shaped) or catastrophic (J-shaped). The former is characterised by the juveniles representing the majority of the assemblage, the prime-age representing the least, and old adult the median (Klein & Cruz-Uribe 1984; Lyman 1994; Steele 2003). The latter is characterised by the juveniles representing the majority of the assemblage with representation decreasing through subsequent categories (Klein & Cruz-Uribe, 1984; Lyman, 1994; Steele, 2003).

The Drimolen *P. robustus* demographic profile does not clearly fit with either the J-shaped or U-shaped model. Even if the "No Dentition in Occlusion", "Deciduous Only", and "Mixed Dentition" categories were amalgamated to create a solitary "Juvenile" category, the "Permanent Dentition Only" (Prime-Age) category would still be the best represented. It is possible that this pattern is indicative of group protection behaviours observed in extant baboons (discussed below in segment 8.4.1). The only comparative populations that also have all five categories represented are the Drimolen baboons and the chimpanzee natural attrition curve. The proportions in which these categories are represented in the latter however, differ greatly from the Drimolen *P. robustus* profile. The Drimolen baboon profile, however, yielded the second strongest result. The age distribution seen in the Drimolen *P. robustus* population is also similar between the Swartkrans Member 1 *P. robustus* population and the extant baboon population. However, the "No Dentition in Occlusion" and "Old Adult" categories are not represented at Swartkrans Member 1 and the "No Dentition in Occlusion", "Deciduous Dentition Only", and "Old Adult" categories are not represented by the extant baboon population.

The Drimolen *Homo* demographic profile appears to adhere to the J-shaped mortality curve model. Despite the Swartkrans Member 1 *P. robustus* profile also consisting of individuals only within the "Deciduous Dentition Only", "Mixed Dentition", and "Permanent Dentition Only" categories, the dispersal of individuals within these categories do not at all resemble that of the Drimolen *Homo* population. The Drimolen *Homo* profile did not yield a result above the set Alpha level with any of the comparative populations utilised here. That said, statistical analysis of the Drimolen *Homo* and the Drimolen baboon as well as the Drimolen *Homo* and the Swartkrans Member 1 *P. robustus* yielded the strongest results against accepting the null hypothesis. Comparison with the extant chimpanzee yielded the highest p-value followed by the extant baboon population and Drimolen *P. robustus* with equivalent results. While differences are still present between the Drimolen *Homo* demographic profiles and those of the extant chimpanzee and the Drimolen baboon, the disparity is not nearly as stark as with the two *P. robustus* populations or the two baboon populations. They are more likely to have

been influenced by sampling bias (discussed below in segment 8.4.2). In fact, all fossil assemblages will be effected by bias, pre-, peri-, and post-deposition.

7.4.1 Predation

In the case of an accumulation caused by the activity of carnivores such as leopards, small mammals (possibly inclusive of infant primates) are often consumed whole and not brought back to a den for consumption (Bothma & Le Riche 1986). This of course, would result in an under-representation of infant individuals deposited as compared to the number of infant individuals deceased. Data collected through direct observation of an extant group would record a higher number of infant deaths, as the loss of these individuals would be documented. That said, studies into the presence of acid-etching on fossil hominin material would inform on the possibility of ingested individuals being deposited through carnivore elimination (Pickering & Carlson 2004). The *P. robustus* deposit at Swartkrans Member 1 is commonly thought to be a carnivore accumulation. This is due to the presence of carnivore material within the deposit, both hominin and non-hominin fossil material exhibiting carnivore tooth marks and acid etching, and studies assessing skeletal element representation (Vrba 1976; Brain 1981; 1993). Carnivore behaviours such as those reported by Bothma and Le Riche (1986) may contribute to the lack of very young individuals in the hominin deposit.

P. robustus would likely have weighed far below the prey preference threshold of the leopard (up to 150 kg; Schaller 1972; Smith 1977; Estes 1991; Bailey 1993; Mills & Biggs 1993) and fossil remains recovered from the Swartkrans Member 1 assemblage display what is undoubtedly leopard tooth marks (SK 54; Figure 44; Brain 1993). Carnivores such as the leopard seem to preferentially kill young, old, and sick or injured prey (Kruuk 1986; Estes 1991; Bailey 1993). A high number of individuals within these categories would be indicative of a leopard accumulation. However, as seen in the baboon predation demography profile, this is not always the case. Particularly with baboons, group behavioural factors influence this mortality profile. In predation profiles among baboons, the Prime Age category is the best represented due to troupe protection behaviours leading individuals within this age category to confront the leopards

(Cowlishaw 1994). Though group behaviours such as defence mechanisms and protection behaviours of *P. robustus* are unknown, factors such as this must be considered when interpreting demographic profiles of extinct populations. Further insight into the timing of the life-history milestones of this species will help to elucidate behavioural details such as these.
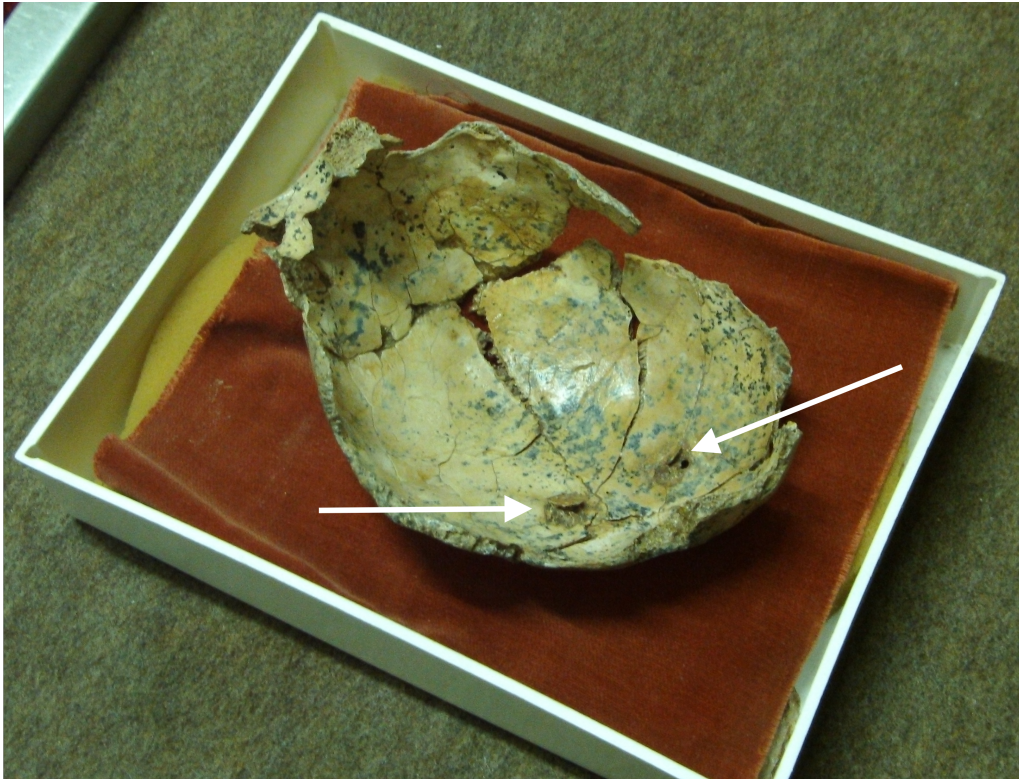
Figure 44: SK 54 with leopard tooth-marks

7.4.2 Preservation and Other Accumulation Models

When studying fossil populations, factors less likely to affect extant populations must be considered. In the case of depositional scenarios such as fluvial transport, recovery is dependant first on the skeletal material moving from the place of death (likely the open landscape) to the cave deposit (Lyman 1994).

Once the skeletal material is deposited, either via non-anthropogenic or autochthonous accumulation processes, the material must then preserve until recovery. The significantly lower bone density of neonatal or infant individuals would contribute to an

underrepresentation of these categories, as the material is less likely to preserve (Lam et al. 1999). The non-hominin faunal assemblage recovered form the Drimolen Main Quarry, however, preserves elements with cortical thicknesses equivalent to that of immature primates (inclusive of hominin species), suggesting the presence of these individuals is unbiased in this way within the Drimolen assemblage (Adams et al. 2016). Differences in excavation techniques, and so recovery, will also affect the demographic profiles of fossil populations. In addition to being heavily disturbed by mining activity, many sites excavated in the early 20th century employed dynamite (Keyser et al. 2000). While this is no longer practiced, differences between material excavated from soft decalcified sediment, material mechanically prepared from hard breccia, and material chemically prepared from hard breccia have different identification and recovery rates. Assemblages recovered from decalcified sediment, as opposed to hard breccia, are more likely to have lost skeletal material through the decalcification process. Materials mechanically prepared from hard breccia are more likely to under-represent small skeletal and dental elements due to the destructive nature of the process. These factors are most likely to affect infant and juvenile material due to its smaller size.

7.5 Conclusions

The demographic profile of the Drimolen *P. robustus* population most closely resembles those of the Swartkrans Member 1 *P. robustus*, the Drimolen baboon, and the extant baboon, respectively. The profile of the latter represents individuals killed through leopard predation. While the extant baboon profile only includes individuals within the Mixed Dentition and Permanent Only categories, this may be an artefact of the baboon behavioural regime. If *P. robustus* did not exhibit group protection behaviours leading prime age individuals to confront the predator, it would be more likely for a predation profile to more accurately represent the prey preferences of the predator.

Additionally, the presence of these other categories within the Drimolen *P. robustus* demographic profile may be indicative of multiple accumulation processes. Its strong resemblance to the Drimolen baboon paleo-population supports this possibility. As the Drimolen baboon assemblage has been suggested to represent a duel depositional process

(Nieudoudt 2015), it is possible that this is also true for Drimolen *P. robustus*. However, as the latter also closely resembles the extant baboon population, known to represent a predation profile, it is also possible that both the Drimolen baboon and *P. robustus* populations represent, at least primarily, a carnivore accumulation.

That said, the Swartkrans Member 1 *P. robustus* profile has also been discussed as a carnivore accumulation. This profile does not include individuals within the No Dentition in Occlusion or the Old Adult categories, unlike the Drimolen *P. robustus* profile. However, as the former category consists of deciduous teeth or permanent tooth buds, it would not be unlikely for these very small elements to be excluded due to a sampling bias caused by recovery techniques utilised at Swartkrans. Additionally, some error is expected within the Swartkrans Member 1 *P. robustus* demography profile as ages have been adapted from Mann (1975) and access to the original material for reassessment could not be obtained.

Statistical analysis of the demographic profile of the Drimolen *Homo*, however, does not support the acceptance of the null hypothesis in any comparison made. This may be due to multiple variables. In part, these results may be due to the small sample size of the current Drimolen *Homo* palaeo-population (n=9). Relative proportions in a sample such as this could easily shift through the addition of only a small number of individuals—for example, if individuals currently attributed to the Indeterminate Hominin category were subsumed into the *Homo* category. That said, the presence of 78% of the *Homo* population within the Deciduous Only category is still worth noting. In particular, a demographic bias of this extreme degree is unlikely to be the result of a sampling error due to a small sample size.

It appears to be the case that carnivore accumulations such as the extant baboon sample or the Swartkrans Member 1 *P. robustus* sample (or, perhaps, the Drimolen baboon and Drimolen *P. robustus* samples), retain a more distinct demographic profile than that of living accumulations as represented here by the extant chimpanzee sample. As this is the case with the populations examined here, it must be noted that the pattern exhibited by

the Drimolen *Homo* showing a very high percentage of individuals in the Deciduous Only category and the low percentage of individuals in the Permanent Only category remains significant and does not fit within the range of variation of those profiles representing predation.

Additionally, the accuracy of comparative populations must be considered. For example, the artificial nature of the wild chimpanzee profile may obscure statistical relationships. That is, the chimpanzee profile, produced through an observational longitudinal study, records every individual lost. Fossil assemblages cannot reflect this scenario accurately as every deceased individual will not be deposited, preserve, and sampled. The added issue of behavioural implications is also inherent in demographic analyses such as this. While predation profiles of extant baboons vary from the typical carnivore model due to group protection behaviours of prime-age individuals, it may also be true that the living/sleeping behaviours of extant chimpanzees are not a fully reliable model for those of early *Homo*.

The presence of archaeology within the Drimolen Main Quarry deposit (Keyser et al. 2000) may also be indicative of a hominin living site. The stone tool assemblage has been proposed to have been manufactured by early *Homo* (Keyser et al. 2000). There is also a collection of bone fragments that have been purported to represent bone tools attributed to *P. robustus* (Backwell & d'Errico 2008) at Drimolen however, a fulsome taphonomic analysis would be required to determine the origins of these specimens. Additionally, a taphonomic analysis of both the hominin and non-hominin fauna would elucidate on the presence of carnivore-tooth marks and other indicators of this method of accumulation as well as assist in identifying anthropogenic materials such as cut-marked bone.

8. Future Directions

The primary goal of this thesis was to conduct a palaeodemographic analysis of the Drimolen hominin assemblage. Palaeodemographic studies, based on the concept of life-histories, play an important role in the interpretation of extinct hominin species. Inspection of life-history characteristics includes species-, and sometimes population-, specific patterns regarding the chronology and synchrony of growth, maturation, and aging milestones (i.e. age at weaning, age at first reproduction, interbirth interval, etc.). Additionally these landmarks can help interpret the behaviour of extinct taxa. As histological studies are just beginning to broaden the understanding of hominin life-history markers and allow for species-specific patterns to be determined, further work in this direction was conducted through the course of this thesis. It has been hypothesised that adaptive strategy is the most influential factor on life-history (Bronikowski et al. 2010). The proclivity for related behaviours to vary due to shifting evolutionary pressures, however, creates a risk of conclusions drawn from temporally and geographically disparate datasets being obscured through regional variation and time averaging. As accepted hominin species—or genera, as they are often assessed—existed on the landscape for hundreds of thousands if not millions of years and across thousands of kilometres, it is a risk even within species-specific studies for results to be variable to the point of meaninglessness. For example, studies discussed previously have presented periodicity times for *Australopithecus africanus, P. robustus*, and early *Homo* that overlap significantly to the point that periodicity cannot be used to determine genus let alone species. While this, of course, may be an accurate result, differences in enamel thickness and absolute dental element size suggests against it. Instead, these results are likely influenced by regional variation and time-averaging within species.

The hominin assemblage at Drimolen is well-suited to this type of assessment as it likely represents a rapid accumulation (Mallett 2015; Herries et al. in prep). Due to this, the individuals within the assemblage can be treated as a palaeo-population. That is, the effects of time-averaging and regional variation are greatly reduced as the individuals would have been on the landscape at approximately the same time and all member of the present species likely exhibited equivalent adaptive strategies as equivalent

environmental pressures would have applied. Additionally, life-history marker identification based on odontogeny and dental histology can be applied to the Drimolen hominin assemblages as the vast majority of the material is represented by dental material.

The goals of this thesis were as follows:

- Evaluate previous palaeodemographic methods
- Present anatomical descriptions and species attributions of the unpublished Drimolen hominin material
- Establish an MNI for *P. robustus* and early *Homo* at Drimolen
- Identify odontogenetic patterns of *P. robustus* at Drimolen through relative seriation
- Present a novel method for quantifiably assessing dental wear
- Assess the palaeodemography of *P. robustus* and early *Homo* at Drimolen

8.1 Evaluate previous palaeodemographic methods

It was hypothesised that previous methods, exemplified in this thesis by Mann (1975), using modern human odontogenetic analogues for the assigning of ages at death to fossil individuals would be inaccurate as compared to histologically determined ages. This hypothesis was supported through comparison of Mann's (1975) age attributions, ages assigned by the author following Mann's (1975) method, and histologically determined chronological ages (Smith et al. 2015).

While consistently erroneous, the degree of error displayed two notable patterns. Firstly, modern human ages attributed to deciduous dentition of *P. robustus* at Drimolen were less inaccurate than those attributed to permanent dentition. This suggests that the developmental pattern of *P. robustus* deciduous dentition was more similar to that of modern human than the developmental pattern of *P. robustus* permanent dentition. It has, however, been suggested that the odontogeny of *P. robustus* deciduous dentition is highly variable as compared to the permanent dentition of the same (Conroy & Mahoney 1991) and this pattern may be an artefact of that.

Secondly, modern human ages attributed to specimens consisting of only isolated dental elements yielded a result with less range than when attributed to specimens consisting of more dental elements. That is, a specimen with one element may be assigned the age of 4 ± 1 years, while a specimen consisting of multiple dental elements may be assigned the age of 4 ± 5 years. This suggests the pattern of development and eruption of one dental element *relative* to another in *P. robustus* is significantly different from the relative internal pattern in modern human. This implies that not only will the application of a modern human analogue produce erroneous ages, but such analogues are not suitable even as basic predictive models of pattern.

8.2 Present anatomical descriptions and species attributions of the unpublished Drimolen hominin material

The primary identification, speciation, and descriptions of the unpublished Drimolen hominin dental material was undertaken via inspection of the original specimens and comparison with other Pleistocene age South African hominins incorporating *Australopithecus sediba, Australopithecus africanus, Homo sp*, and *P. robustus*. These descriptions followed Moggi-Cecchi et al. (2010).

8.3 Establish an MNI for *P. robustus* and early *Homo* at Drimolen

The MNI was calculated on the basis of the most abundant element count, (dentition), and by taking account of ontogenetic stage of development, wear and metrical data.

8.4 Identify odontogenetic patterns of *P. robustus* at Drimolen through relative seriation

Once an MNI was determined, the Drimolen hominin material was seriated based on relative age to avoid applying extant analogues. Relative age was based on developmental and wear stages. The individuals were assessed based on these stages and placed into five categories for demographic interpretation. Assessing the population in this manner avoids errors inherent in assigning exact ages beyond the scope of quantitative methodologies. Utilising both the exact ages presented by Smith et al. (2015)

and the relative age seriation of the Drimolen *P. robustus* material, dental development patterns specific to the species were examined. The ages at which particular odontogenic landmarks occur are crucial to determining life-history traits. Though results produced are preliminary, the supplementing of histological studies with some relative comparisons appear likely to elucidate these key developmental stages. To include older individuals in these interpretations, a wear analysis was conducted.

Any observations or conclusions drawn here are preliminary. Histological analyses (e.g. Smith et al. 2015) are laying the groundwork for exact, precise, species-specific patterns. However, determining exact ages at death requires a methodology that can only be applied to a small sample of individuals at a specific stage of development (Smith et al. 2015). Consequently, this limits the methodology to a specific range of life-history. In *P. robustus*, this means the di1, di2 and dc are already in occlusion at the youngest end and the P3, P4, M2, and M3 are not yet erupted at the oldest end. It may be possible, however, to examine long-period line striations in a manner similar to Smith et al. (2015) to expand the focal point of these studies. Striation irregularities due to stress can be linked across all dental elements forming at the time; Smith et al. (2015) utilised this technique. If applied in combination with isotopic studies, the formation and eruption pattern and rate of deciduous dentition could be determined. Isotopic studies can identify changes in diet such as weaning (Sponheimer et al. 2006). An equivalent striation or series of striations across multiple dental elements would indicate the disparity in developmental stage between the elements (Lacruz et al. 2008). Coupled with periodicity and chronological age studies, the exact length of this disparity could be calculated to produce an accurate species-specific pattern of formation.

An expansion of the study to include *P. robustus* from other sites such as Swartkrans Member 1 and Kromdraai B is crucial to verifying these results. Not only would this greatly increase the sample size, but it would also provide a better representation of intraspecific and individual variation. The Swartkrans Member 1 *P. robustus* material varies slightly but consistently in metrical data from the Drimolen *P. robustus* assemblage (Moggi-Cecchi et al. 2010). It includes a significant number of more

complete specimens (Brain 1993), and inclusion would increase the number of individuals attributed with exact histological ages (Smith et al. 2015).

8.5 Present a novel method for quantifiably assessing dental wear

It proved possible to quantify post-canine wear for the purposes of determining exact ages. Supplementing the method tested in this study with biomechanical studies of masticatory forces and rate of enamel loss could be used to determine exact ages at death for fossil individuals. Additionally, as indicated by the preliminary wear analysis, important life-history traits can potentially be identified this way (age at weaning; interbirth interval). The application of a quantifiable method of recording occlusal wear to a sample of individuals assigned histologically-based chronological ages at death will also allow for an estimation of *rate* of wear. Determining the rate of wear, while allowing for the identification of behavioural changes reflected in changes in the rate of wear, will also allow for a predictive model of wear used to estimate chronological ages in a non-destructive, non-intrusive manner that is not limited to a specific state of development as are histological studies (e.g. Smith et al. 2015). The addition of the Swartkrans *P. robustus* material, as is the case with the other studies within this thesis, will help to facilitate these determinations by increasing the sample size both to incorporate more variability but also more individuals assigned chronological ages.

8.6 Assess the palaeodemography of *P. robustus* and early *Homo* at Drimolen

The age profiles of the Drimolen hominins established were then assessed against *P. robustus* from Swartkrans Member 1, a natural attrition profile of wild chimpanzee, a predation profile of wild chacma baboons, and the Drimolen fossil baboon population. It was found that the Drimolen *P. robustus* demographic profile most closely resembled that of the Swartkrans Member 1 *P. robustus* population, thought to, at least in part, represent a carnivore accumulation. Contrastingly, the Drimolen early *Homo* demographic profile did not strongly resemble any of the comparative populations. That said, a multitude of variables can assist the determination that the Drimolen *Homo* palaeo-population does not represent a carnivore accumulation and may, in fact, represent a living site accumulation. The possible identification of differential accumulation

methods at Drimolen for early *Homo* and *P. robustus* has significant implications for understanding how caves were used by different hominin species at different times and how these species were behaving on the landscape. In particular, the possibility that early South African *Homo* was utilising caves for 'living sites' would provide new information through which to interpret the possible behavioural repertoire of this poorly represented taxa.

It has been suggested that *P. robustus* would have displayed group behaviours similar to those of the extant baboon (Jolly 1970; Lockwood et al. 2007), however this cannot be confidently concluded. It has also been suggested that sub-adult males would leave the group as seen in harem-based ape populations, making them more vulnerable to predation (Lockwood et al. 2007). Behaviours such as these would be supported by conclusions drawn based on demographic analysis as both the Drimolen and Swartkrans Member 1 *P. robustus* profiles resemble that of the extant baboon predation profile applied in Chapter 7. Life-history data such as length of childhood, interbirth rates, and the presence or absence of secondary male maturation (the silverback effect) would be crucial to interpreting group behaviours and how they would affect predation mortality profiles. Refinement of age at death, dental development patterns, and determination of age at weaning through methodologies proposed in previous chapters would contribute to the base of knowledge necessary to make these interpretations. While carnivores have been identified within the Drimolen assemblage (O'Regan and Menter 2009), a full taphonomic of all fauna present would be crucial to understanding the depositional processes, and so demographics of all species recovered from the site.

8.7 Future Work

This study has provided the groundwork necessary for the interpretation of the Drimolen Main Quarry hominin assemblage, as well as assessed and presented methodologies for the purposes of clarifying the life-history of *P. robustus* and early *Homo*. Palaeodemographic interpretations are crucial to the understanding of extinct taxa. Many analyses are dependent upon variables linked with demographics. Population size, sex ratios, lifespan, length of childhood, and interbirth intervals are all examples of life-

history variables that affect group behaviours. It is necessary to understand group behaviours to confidently interpret taphonomy, the geographic range of a population, diet and behaviours associated with resource acquisition, and other characteristics more easily determined in extant populations. Due to the strong correlation of dental development and life-history traits (Dean et al. 2001), as well as the over-representation of dental material in the fossil record, the study of odontogeny is the logical starting point when addressing these questions.

Analyses conducted in this study, while largely preliminary, have been successful and show potential in expanding the current body of knowledge in regards to hominin life-histories. Expansion of these analyses to include *P. robustus* palaeo-populations from Swartkrans Member 1, for example, would greatly increase the confidence in which conclusions can be drawn. The inclusion of the Swartkrans Member 1 *P. robustus* material into the relatively aged sample would be valuable for identifying odontogenetic patterns. Future work in this vein would help to identify the sensitivity of odontogeny and life-history. As Swartkrans and Drimolen are within 10 km of each other and the demographic studies presented in Chapter 7 indicate similar age at death profiles, differences identified in odontogenetic pattern between these two *P. robustus* palaeo-populations could be used to interpret adaptive strategy disparity. Any Swartkrans material utilised in this manner, however, would first need to be relatively seriated as detailed in this thesis. Current age at death attributions are drawn from modern human ages (Mann 1975) and so are inaccurate, as shown in Chapter 3. Additionally, the Swartkrans Member 1 *P. robustus* material contains a higher number of individuals consisting of more than one element. The addition of this to the Drimolen *P. robustus* sample used in this study would provide the opportunity to further clarify odontogeny of the species. This provides the opportunity to not only increase the sample size examined but also to increase the variability of the sample, as these assemblages differ in standard metrics (Moggi-Cecchi et al. 2010). A larger and more diversified sample would greatly increase the likelihood of these analyses yielding accurate and precise results.

The inclusion of more complete individuals belonging to the Swartkrans Member 1 *P. robustus* assemblage would also be beneficial to the quantifiable wear method proposed in Chapter 6. Variables such as bilateral dissymmetry and maxillary-mandibular dissymmetry could be more thoroughly examined. As the histological aging method has also been applied to a portion of the Swartkrans material by Smith et al. (2015), the number of individuals with exact ages at death would also increase allowing for further estimates of wear *rate* as well as pattern.

Additional methodologies would solidify conclusions drawn in this study. One such methodology is the biomechanical analysis of the *P. robustus* masticatory apparatus for the purposes of determining rate of enamel loss to exactly age individuals based on stage of wear. Another applies isotopic and microstructural analyses to determine both age at weaning and the exact stages of development of elements relative to one another for the purposes of determining an accurate species-specific odontogenic pattern.

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Appendix 1: Dental Anatomy
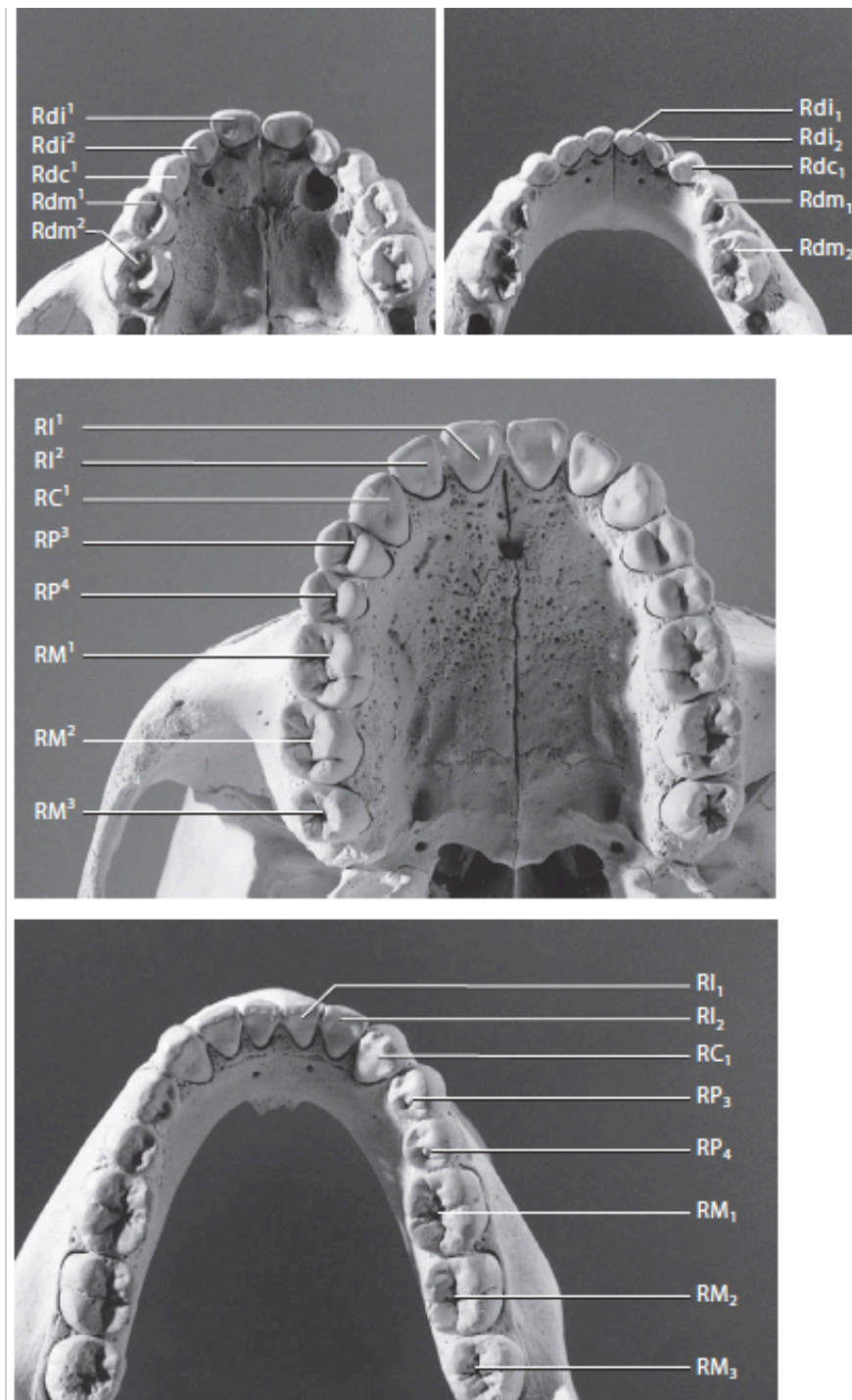
Dental Arcade Element Identification: (top) deciduous and (middle & bottom) permanent; Adapted from White & Falkens 2005
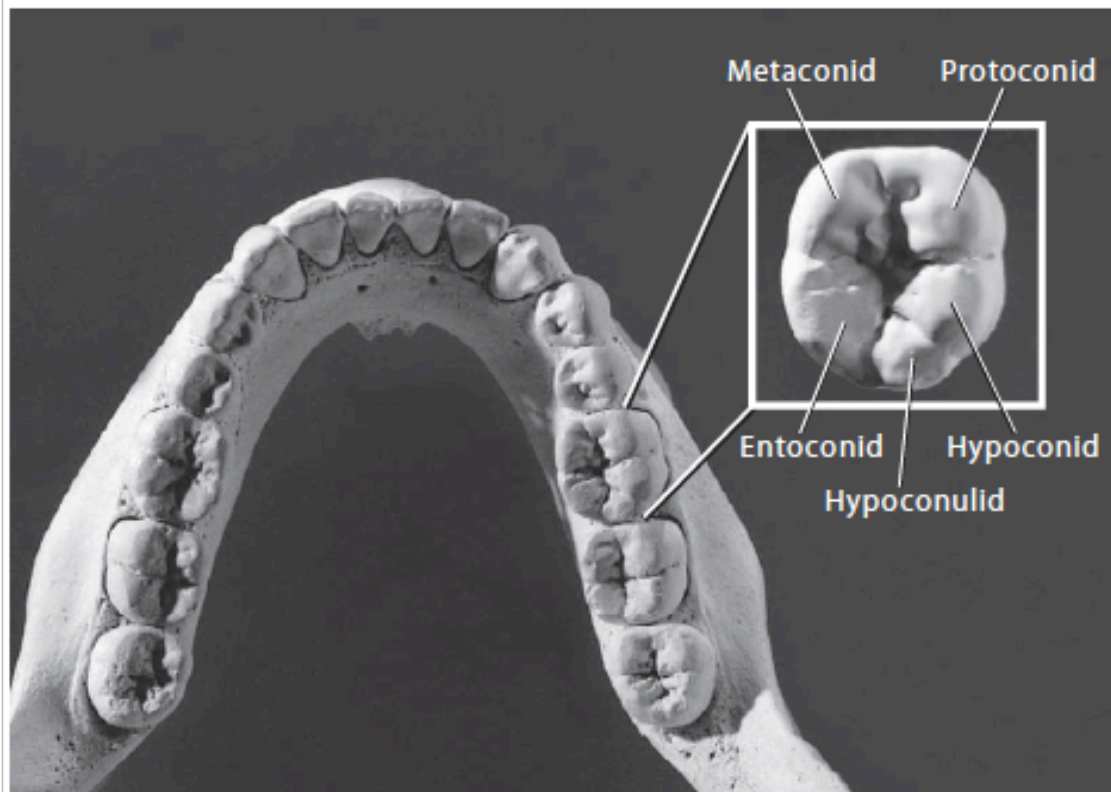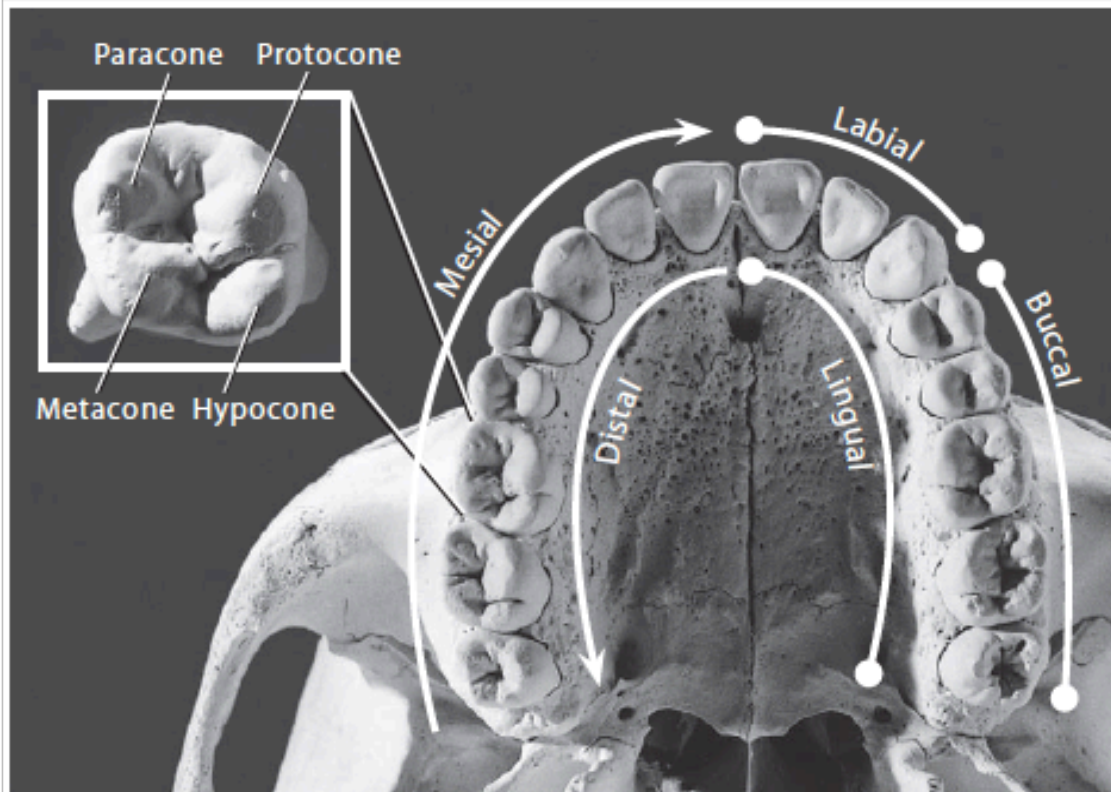
Dental Directional Terminology with Molar Cuspal Terminology Inset; Adapted from White & Falkens 2005
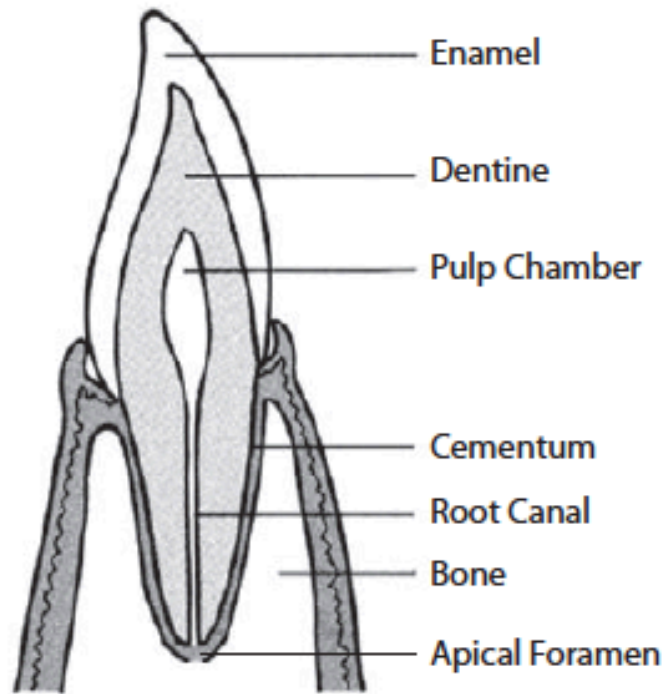
Anatomy of a Tooth; Adapted from White & Falkens 2005
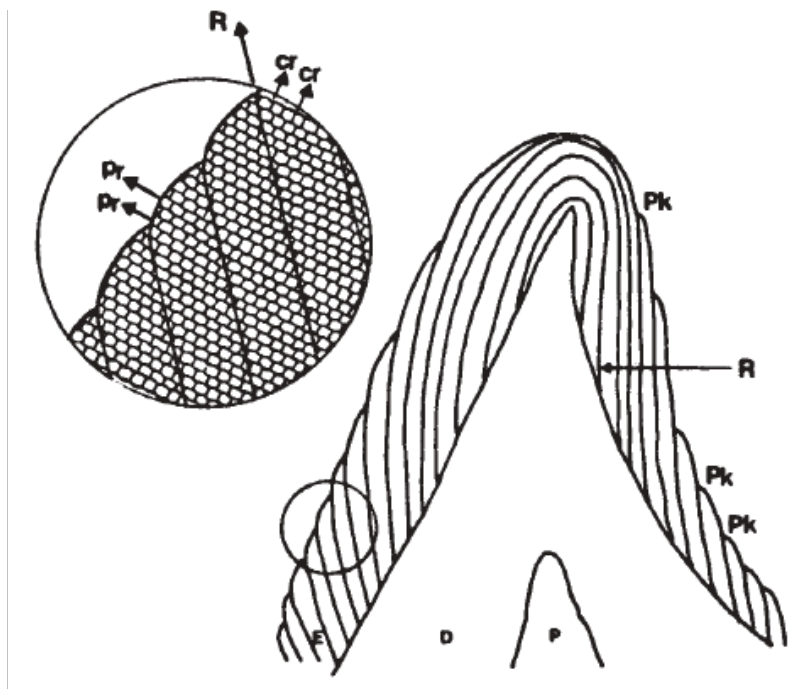
Internal Structure of a Tooth: (E) Enamel; (D) Dentine; (P) Pulp; (R) Striae of Retzius; (Pk) Perikymata; (Pr) Enamel Prisms; (Cr) Cross-Striations; Adapted from Bromage & Dean 1985

Appendix 2: Anatomical descriptions of unpublished Drimolen hominin dental material

Descriptions have been sorted into three categories by author. Category 1: Written by Jacopo Moggi-Cecchi; in prep. Category 2: Written jointly by Jacopo Moggi-Cecchi and the author (Angeline Leece); in prep. Category 3: Written by the author (Angeline Leece).

"Abbreviations include: ICF=interproximal contact facet, BL=buccolingual or labiolingual, MD=mesiodistal, M=Mesial, MB=mesiobuccal, DB=distobuccal, L=lingual, ML=mesiolingual, DL=distolingual, IC=incisocervical, DMR-distal marginal ridge, MMR=mesial marginal ridge, and DEJ=dentino-enamel junction. Root lengths are in mm." (Moggi-Cecchi et al. 2010, pp. 1)

Category 1:

DNH 7: Skull (a) and mandible (b), both with complete dentition

Mandibular teeth.

LI1. Preservation of the left tooth is good the root is partly exposed. The right has the crown cracked, and the mesial half largely missing. Wear is marked, with crown height reduced. A single, large area of dentine is exposed, with a thick enamel rim still preserved. The wear plane is lingually bevelled. The preserved portion of the labial face is MD convex. No strong cervical eminence is evident. The root is long and thin. The exposed part of the root is 14,8 mm.

RI2. Both teeth are well preserved. Wear is marked, with crown height reduced. A single, large area of dentine is exposed, with a thick enamel rim still preserved. The wear plane is lingually bevelled. The preserved portion of the labial face is MD slightly convex. The cervical eminence is straight. The lingual face is unremarkable.

RC. The left canine shows longitudinal cracks, the right is well preserved. Wear is marked, with cusp height reduced. The worn surface is round. Dentine is exposed surrounded by a thick enamel rim. The wear plane is tilted slightly distally. The labial face is markedly convex MD. The enamel line is concave. There is no enamel hypoplasia. The lingual face shows moderate cervical eminence. Remnances of the depth cleft delimiting a thick DMR are evident.

LP3. Preservation is good. The occlusal surface is worn flat. Small areas of dentine are exposed on both the buccal and lingual cusps. The occlusal outline is oval. Wear obscures the morphological details. The buccal face is markedly swollen. The cervical enamel line is V shaped.

LP4. Preservation is good. The occlusal surface is worn flat. Small areas of dentine are exposed on both the buccal and lingual cusps. The distal face is worn by interproximal attrition. A tiny enamel chip (flaked away in life) is missing from the distal edge of the crown. The occlusal outline is oval with a marked distolingual extension. The right tooth is almost square in outline. Although worn, the protoconid is larger than the metaconid. The posterior fovea is reduced to a thin fissure. The DMR appears to have been very thick. The buccal face is moderately swollen. The cervical enamel line is markedly V shape. The lingual face is unremarkable.

LM1. On the right tooth the disto-buccal corner of the crown is missing. Part of the mandibular body at the level of M1 is missing, exposing the internal part of the body. The roots are missing. The left tooth is well preserved. Wear has exposed dentine on the buccal cusps and the metaconid. Round and concave basins are evident on the protoconid and metaconid. The entoconid is worn flat. The mesial and the distal faces are worn by the interproximal attrition. Two enamel chips flaked away from the distal edge of the crown. The occlusal outline is almost square. Wear does not allow the morpholigical description. The only remarkable feature is the Y-pattern form by the cusps. On the buccal face the cervical enamel line is V shape.

LM2. Preservation is good. On the right tooth the root is partly exposed, showing the mesial root tip broken. The occlusal surface is worn flat but there is no dentine exposed. Mesial and distal interproximal attrition is marked. A small enamel chip is missing from the distal edge. Occlusal outline is square. The cusps form a Y-pattern. A small C6 is present. On the buccal face the cervical enamel line is V shape.

LM3. Preservation is good. The main cusps are worn flat, apart from the metaconid, with rounded cusp. Attrition on the mesial faces has produced a concave facet. The occlusal outline is oval tapering distally. The main cusps are well delineated. The metaconid is the largest cusp, followed by protoconid, hypoconid, entoconid and hypoconulid in decreasing size. The cusps form a Y-pattern. A large C6 is evident. A small but well

defined C7 is evident. The MMR is thick. There is no anterior fovea. The longitudinal fissure is very deep. The central fovea is small and deep. The posterior fovea is deep and it is largely occupied by the C6. On the buccal face the mesial buccal groove is short and deep, ending in to a pit. An incipient protostylid is evident. The distobuccal groove is also short and deep.

Maxillary teeth.

I1. On the right tooth only the mesial half of the crown is preserved. The root is in the bone. On the left tooth there is a longitudinal crack on the crown and an enamel chip missing on the mesial-lingual corner. Attrition has markedly reduced crown height. A large rectangular area of dentine is exposed on the incisal edge, with relatively thick enamel rims. The wear plane is tilted distally. Both the mesial and the distal edges of the crown are worn by interproximal attrition. The labial face is MD flat in its central portion, with rounded corners. The enamel line is gently convex. The lingual face has a V-shaped outline, with no cervical eminence. Both the MMR and the DMR are very faintly expressed. The root is thick, long and straight, conical in shape. Its length is 16.4.

I2. Preservation is good. Crown height is markedly reduced by wear. A large area of dentine is exposed. The wear plane is tilted both distally and labially bevelled. Interproximal attrition is marked. The labial face is convex MD. On the lingual face the cervical eminence is faint. Both the MMr and the DMR are well developed, merging at the cervical eminence.

C. Preservation is good. The root of the RC is partly exposed. The cusp is worn flat. A round and concave dentine basin is exposed. A relatively thick enamel rim is evident. The wear plane is flat, with a slight distal tilt. The mesial ICF is on the mesio-lingual corner of the crown. On the right tooth it is located on the labial face. The labial face is markedly convex MD. The CEL is almost straight. The lingual face is faintly swollen at its cervix. Remnants of a deep cleft adjacent to the thin MMR are evident. The exposed portion of the root is very thick and long. Root length of the RC is 23.2 ca.

P3. The right tooth is well preserved. On the left tooth, only a distal fragment of the crown is preserved. Wear is marked, with a large, oval area of dentine exposed on the paracone, and a round, smaller, on the protocone. Interproximal attrition with the canine

has produced a large BL concave facet. The distal ICF is also large. No morphological details can be described. The buccal face is markedly swollen.

P4. The right tooth is well preserved. The left tooth shows only minor cracks on the crown. The buccal roots are exposed. The occlusal surface is worn flat. Small areas of dentine are exposed on both the buccal and the lingual cusps. Both ICF are large. The occlusal outline is oval. No morphological details can be described. The buccal face is markedly convex OC. The cervical enamel line is V shaped. The exposed buccal roots are long and thin. Their apex is distally tilted.

M1. Preservation is overall good. On the right crown there is a crack through the protocone and the hypocone. On the left tooth the buccal roots are exposed. A large area of dentine is exposed on the PR. Smaller areas are evident on the PA and the HYP. There is no dentine exposed on the ME. Both ICF are large, reaching the occlusal margin. The occlusal outline is rhomboidal. The PR is judged to be the largest cusp, followed by Pa, ME and HYP, of similar size. Wear obscures morphological details. On the buccal face a small parastyle (sensu PVT, 1991 p. 634) is evident. The cervical enamel line is V shaped.

M2. Preservation is good. The occlusal surface is worn flat, with the main cusps still evident. The mesial ICF is large, encroaching the occlusal margin. The occlusal outline is almost square. The PR is the largest cusp, followed by the PA, HYP and ME. The central fossa is deep. Although worn, an interrupted crista obliqua is evident. The posterior fovea is small and deep, bounded by a thick DMR. On the buccal face, the buccal groove is deep and long, ending with no issue. On the lingual face, the lingual groove is short and deep.

M3. Both teeth are well preserved. On the left tooth the DB roots are partly exposed. Occlusal wear is marked, with the lingual cusps worn flat, and the buccal cusps notably reduced in height. The occlusal outline is square, tapering distally. The PR is by far the largest cusp, followed by the PA, ME and HYP. A marked C5 is evident, especially on the RM3. The central fossa is broad and deep. The crista obliqua is interrupted by a deep groove. The posterior fovea is deep and small, reduced in size by a well-developed DMR. The latter is cut by a groove moving onto the distal face. On the buccal face the buccal groove is faint. The exposed DB root is tilted distally.

DNH 27 (b) RP4 (c) RM1 (initially labelled DNH 98)

This specimen comprises two isolated, associated teeth, a RM1 and a RP4

RP4. This tooth is the antimere of DNH 27, now re-labelled 27a . Despite differences in colour with DNH 27a (a LP4) this specimen is almost identical in overall morphology, wear, roots number, and dimensions of crown and roots. Description of DNH 27a is given in Moggi-Cecchi et al., (2010). For convenience, the description of the tooth is repeated here. Preservation of crown and roots is very good, except for minor cracks crossing the occlusal surface, worn flat with dentine areas exposed on the protoconid and the metaconid. Tiny dentine pits are also visible on the talonid, on the buccal and the lingual side. Both the mesial and the distal ICFs are large, reaching the occlusal surface and markedly reducing the original MD dimension. The mesial ICF faces mesio-lingually, whereas the distal one faces distobuccally. This condition suggests that the premolar was slightly rotated in its position in the tooth row. The occlusal outline is almost square. The talonid is large. No morphological details can be described. On the buccal surface remnants of a deep distobuccal groove are evident. Enamel extensions are evident on the buccal and the lingual face. Both the mesial and distal roots are very long and thin and have two distinct canals. The mesial root is tilted distally. Their length is as follows: M 19.9 and D 18.7.

RM1 . The tooth is well preserved, except for a fragment of the crown missing from the mesial face. The occlusal surface is worn to a flat table. Dentine is exposed on all cusps. This has created a single large basin on the protocone, metaconid, hypoconid and hypoconulid. The distal ICF is very large, and occupies most of the face. No morphological details can be described. Enamel extension is evident on the lingual face. The mesial roots are very long, thin and the apex is tilted distally. They are partially fused, although the two root canals are evident. Similarly, the distal roots are completely fused, straight and the apex tilted distally. Root length is: ML 16.6 MB 16.6 DL 16.9 DB 17.3

DNH 35: Right mandible with dm1, dm2, M1, Ldm2, left radius and ulna (Fig. x). This specimen comprises a fragment of a right mandibular body with well preserved dm1, dm2 and the developing M1. The Rdm1 and Rdm2 are displaced one relative to the other. The isolated Ldm2 is also associated.

dm1. The crown is well preserved. The exposed mesial roots have the MB canal broken. The crown is very slightly worn, with an enamel facet on the mesial edge of the protoconid. The mesial ICF is small and round in shape. The distal ICF is relatively large and oval, reaching the occlusal margin. The occlusal outline is trapezoido-rectangular, with a reduced mesiolingual corner. The five principal cusps are well developed, with the protoconid and the hypoconid as the largest, followed by metaconid, entoconid and hypoconulid in decreasing order of size. The cusp tip of the protoconid is slightly mesial to the metaconid. The MMR is thin and low, and it is separated by the metaconid by a fissure. The anterior fovea is Y shaped and it opens mesiolingually. The distal trigonid crest is ? reduced ?. The central fovea is broad and shallow. There is no fovea posterior. In buccal view, the trigonid is taller than the talonid. On the buccal face a marked tuberculum molare is evident, with a strong cervical convexity. The buccal groove is deep ending into an enamel extension, almost a cingulum, from the hypoconid. Lingually, the lingual groove is a short but deep cleft. A small fissure, distal to the metaconid cusp tip delineates an incipient postmetaconid. The single mesial root has a flat root plate. Preserved root length is 7.3.

dm2. The left tooth is well preserved. The right tooth has the mesial edge of the crown, including the anterior fovea, slightly detached in a mesial direction from the rest of the crown. Also, a subvertical crack crosses the lingual face of the entoconid. On the right tooth the roots are partly exposed and crushed; on the left tooth the root system is well preserved, only missing the MB root. The description refers to the left tooth. Occlusal wear is minimal, with rounded cusps. The ICF is oval, near the occlusal margin. There is no distal ICF. The crown has an ovo-rectangular outline with a reduced distobuccal corner. The five main cusps are well developed. The metaconid is the largest cusp, followed by hypoconid, protoconid, entoconid and hypoconulid. The protoconid tip is

slightly mesial to the metaconid tip. There is no C6 or C7. The cusps form a Y pattern. The MMR is relatively thick and low. CHK mesioconulid e fissure from the anterior fovea to the mesial face. CHK. The fovea anterior is a transverse fissure delimited distally by an incised, narrow trigonid crest. The central fovea is broad and deep. The DMR is fairly thick andnot very high. The fovea posterior is a deep slit. Distal to the apex of the metaconid there is a deep pit delineating an incipient postmetaconulid. On the buccal face just below the protoconid tip, a short transverse furrow is evident. (? Protoconidal cingular furrow FEG?? CHK) The mesiobuccal groove is broad, deep and short. It ends abruptly into a a pit on the edge of which an incipient cuspulid is present. The distobuccal groove is deep and ends gradually. On the lingual face, the lingual groove is short and faint. The ML root is relatively short and thin, straight, subconical in shape. The distal root has a single long, thin and flat root plate. The DL root projects distally. Their length is ML 9.4, DL 6.8 DB 9.2.

M1. The tooth is well preserved. It was unerupted. The crown is complete. There is no root development. The crown outline is an elongated oval. The five principal cusps are well developed with pointed tips. All are of nearly equal size; only the protoconid is slightly smaller than the others. There is no C6. A tiny but well defined C7 is evident. The cusps form a Y pattern. The MMR is thin and low, cu by a fissure in its central part. The fovea posterior is large, bounded by enamel ridges emanating from the apices of the protoconid and the metaconid. As in the dm2, a postmetaconulid is evident. The central fovea is broad. Ht eposterior fovea is small but deep, bounded by a thin and low DMR. Distal to the entoconid cusp tip, an almost distinct cuspulid is evident. On the buccal face, a faint transverrse groove is present on the protoconid. The mesiobuccal groove is deep and broad, ending into a deep pit. A thin protostylid is present. The V-shaped distobuccal groove is deep and short, ending gradually. On the lingual face two parallel furrows delimit the C7.

DNH 47: Left maxilla with di1, dc, dm1, dm2, M1 (bud); right maxilla with di2, dm1, I1 (bud); Rdm1

This specimen comprises the left and right maxilla of a juvenile individual. The left maxilla has di1, dc, dm1, dm2, M1 (bud); the right maxilla has dm1, I1 (bud). Also the associated isolated Ldi2, Rdm1, Rdm2 are present.

di1. This isolated tooth is well preserved, with a minor crack crossing the mesial face. Wear has exposed a strip of dentine on the incisal edge. There is a small, rounded mesial ICF CHK near the incisal edge. The distal ICF is small. The short labial face is almost straight MD and slightly convex IC. The worn incisal edge is sloping distally. On the lingual face, the strong cervical eminence is symmetrical, originating a thick and short median lingual ridge whose axis is tilted mesially.the MMR is faint. The DMR is relatively thick. A V-shaped groove is present between the DMR and the median lingual ridge. The root is long (11.1) conical in shape, subtriangular in section. Near the root tip is is BL compressed. The root tip is tilted lingually.

dc. the tooth preserved only the labial face of the crown. The root is intact. The labial face is moderately convex MD, less so IC. Both the MMR and DMR are present, faintly developed. The root is relatively thick. It is oval in section, with some MD compression. Faint grooves are evident on the mesial and labial face. The root is still open. Its length is 7.8.

dm1. Both the right and left antimeres are present. The left tooth is in the maxilla, its crown broken and most of its fragments missing. The roots are intact. Description refers to the right tooth, which is isolated. The crown is well preserved, apart from a few enamel flakes missing from the base of the metacone and of the hypocone. Wear is minimal, with tiny enamel facets on the main cusps. There is no mesial ICF. The occlusal outline is almost square, with a marked mesio-buccal extension. The four main cusps are evident. The protocone is the largest, followed by the paracone and metacone of approximately the same size, whereas the hypocone is markedly reduced. A strongly developed parastyle is clearly evident, continuous with a thick MMR. There is no anterior fovea. The central fossa is broad and not very deep. The crista obliqua is thick and low, incised in its central part. . The fovea posterior is at a different level from the trigon. It is

a small, deep, transverse fissure, bounded by a thin DMR. No additional cuspules are evident. A well defined enamel shelf moves from the tip of the metacone buccally and then distally, merging with the DMR. On the buccal face, the mesiobuccal groove is short and shallow, delimiting the parastyle. The distobuccal groove is less developed. On the lingual face, the lingual groove is deep, ending with no issue. A Carabelli trait is present in form of a tiny cuspule. The roots are still open. The buccal roots are thin and straight, oval in section with marked MD compression. The lingual one is conical in shape, widely divergent from the others. Preserved root length is MB 6.5, DB 7.9, L 6.8.

dm2. Only the left tooth is present. The crown is well preserved and unworn. The tooth was not yet erupted. Only few mm of the developing roots are present. The occlusal outline is square. The main cusps are well developed. The protocone is the largest followed by the paracone, metacone and hypocone of approximately the same size. The MMR is not very thick and low. Several incipient cuspules are present. The anterior fovea is a long, transverse fissure. It is delimited distally by a ridge of enamel moving from the tip of the paracone parallel to the MMR. The central fossa is broad and deep. The crista obliqua is thin and low, cut at its lowest point by the longitudinal fissure. The posterior fovea is broad and deep. The DMR is low and thin, bearing two ill-defined cuspules. On the buccal face, th buccal groove is short, ending into a pit CHK delimited by a small enamel shelf. On the lingual face the most remarkable feature is a strongly developed Carabelli trait in form of an enamel cingulum. From the lingual margin of the MMR it crosses obliquely the lingual face of the protocone reaching the base of the deep lingual groove. On the mesio-lingual corner, a tiny, but well defined cuspule is present.

I1 this is the developing crown of an upper central incisor. Crown formation is half complete. On the labial face enamel shows 'pavement cracking' On the preserved portion of the labial face both corners are rounded, the distal more than the mesial. In lingual view, the mesial corner appears more angulated, whereas the distal is more rounded.

M1 This is a developing crown, half complete. The entire surface shows immature enamel, with 'pavement cracking' appearance. The main cusps are already delineated, with tall cusps tips.

di2. The tooth is isolated and well preserved. Incisal wear is minimal , with a thin strip of dentine exposed on it. The mesial ICF is large and elongated. The distal ICF is small, drop shaped. The labial face is almost straight. The outline is asymmetrical, with the mesial shoulder more angulated and the distal more rounded. On the lingual face the cervical eminence is marked, symmetrically disposed. Both the mesial and the distal marginal ridges are relatively well developed. A faint ridge is evident mesially to the midline. The root is oval in cross-section, with some MD compression. It is long and thin. A faint groove is evident on the distal face. Its length is 10.1.

dm1. This tooth is isolated. Its crown and roots are well preserved. Only a tiny flake of enamel is missing at the base of the distal face. The roots are partly damaged in the lower half. Wear has produced small enamel facets on the buccal cusps. There are no mesial and distal ICF. The occlusal outline is almost drop-shaped. The five principal cusps are well developed. The metaconid is the largest, followed by protoconid, hypoconid, entoconid and hypoconulid in decreasing order of size. The protoconid cusp tip is placed slightly mesial to the metaconid. There is no mesioconulid. The MMR is relatively thick and low, continuous to the metaconid. On its buccal end, it project mesially. The anterior fovea is a short and deep fissure. The central fovea is broad and shallow. The posterior fovea is occupied by a small but well delineated C6, emanating from the center of a thin DMR. In buccal view, the trigonid is taller than the talonid. On the buccal face, the tuberculum molare is poorly developed. Cervical swelling is more marked on the hypoconid. The buccal groove is very deep, extending over the entire face. Near the occlusal margin, it enlarges into a pit, delineating an incipient protostylid. On the lingual surface, the lingual groove is faint but long. The roots are relatively thin. They are divergent in a MD direction. There is a single mesial and a single distal root, both with a long root plate. The mesial root plate is MD compressed in its central part, for its entire length. The distal root is oval in cross section.

Rdm2 .

This is an unworn tooth with excellent preservation. The tooth was not yet erupted. Only few mm of the developing roots are present.The crown has an ovorectangular occlusal outline, with a marked buccal extension at the base of the hypoconid. All five principal cusps are well-developed, with the metaconid being the largest followed by the hypoconid, protoconid, entoconid and hypoconulid. The main cusps form a Y occlusal pattern. Numerous additional cuspulids are present. On the metaconid two grooves clearly delineates a postmetaconid and, distal to it, a postmetaconulid. The latter cannot be considered as a true C7 since it is not completely separated from the adjacent cuspulid /postmetaconid. The MMR is thick and low. It bears a series of five tiny cuspulids. The fovea anterior is a thin and deep fissure, bounded by an accessory/distal trigonid crest. The latter is deeply incised by the longitudinal fissure. The presence of the an accessory/distal trigonid crest creates what is sometimes referred to as a double fovea anterior. The central fossa is both broad and deep. The fovea posterior is deep. The DMR is thick and low. It bears a small but well defined C6. On the buccal face there is a small but marked protostylid. It originates from the base of the hypoconid and moves mesially onto the protoconid. It is incised at the level of the mesiobuccal groove. The mesiobuccal groove is deep and ends in a pit. A marked swelling is evident at the base of the hypoconid. On the lingual face, the lingual groove is faint. On the buccal, mesial and lingual faces many hypoplastic pits are present.

This specimen is considered as part of the same individual DNH 47. It derives from the same square, 40 cm below. It has a similar developmental stage as the upper dm2 (unerupted, crown complete, root initiated 1.5-2.0 mm), similar staining, similar pitting hypoplasia, similarly developed extra cusps,

DNH 77b. RC

This is an isolated and fairly well-preserved tooth. An enamel chips is missing from the labial face. The lingual edge of the occlusal margin is damaged. A crack crosses the occlusal surface and it continues over the labial surface of the root up to the root tip. A

flake of cementum is missing on the mesio-labial corner of the root. The crown is heavily worn. This wear has markedly reduced the crown height and exposed a large, subtriangular area of dentine. The large, flat wear plane is lingually and distally tilted. A very thin enamel rim is evident on the labial edge. On the labial face only a few mm's of enamel are preserved. The enamel line is concave. The long and straight root is subtriangular in cross-section, MD compressed. Longitudinal grooves are present on both the mesial and distal faces. The root tip is tilted lingually with some degree of resorption. Root length is 22.2.

This specimen is most probably associated with DNH 77 since they are both very worn, both are stained with manganese and both show some degree of root resorption.

79b. LC

This specimens is an isolated and well-preserved tooth that is unworn. Only a flake of enamel is missing from the lingual face, on the cervical eminence. Some 7 mm of the root are preserved. Morphological features of the crown and the marked hypoplastic line on the labial face clearly indicate that this specimen is the antimere of DNH 79. For convenience, the description of the tooth is repeated here. This is an isolated tooth that preserves both the crown and the root. The crown is intact, with minor cracks. Some 6.8 mm's of the still developing root are present. Preservation is good, apart from some abrasion on the labial face. The tooth is unworn. The labial face is tall and convex IC and MD. The crown outline is asymmetrical. The crown tip is centrally placed. The mesial edge is short and angled. The distal edge is longer than the mesial edge and more steeply inclined. The MMR is faint, whereas the DMR is marked, giving rise to an incipient stylid with a deep mesial furrow. The cervical enamel line is straight. A marked line of hypoplasia is evident in the cervical third of the crown. On the lingual face, the cervical eminence is moderately developed. It is distally positioned in respect to the midline and gives rise to a marked DMR with a thin edge. The median lingual ridge is slightly developed, but has a sharp crest. The latter, along with the DMR delimit a deep and V-shape cleft. The MMR is relatively faint. The root is thick and oval in section, with MD compression on the mesial face where a subvertical groove is present.

DNH 83: Rdm1

This is a well-preserved deciduous tooth. A crack crosses through the distal cusps. The tooth appears to have just erupted in the mouth although not completely (NEEDS TO BE CLEANED A BIT MORE AT THE BASE ESPECIALLY ON THE DISTAL SIDE. APPEARS IT WAS STILL COMING OUT IN THE MOUTH. STILL TILTED. MESIAL CUSPS SLIGHTLY WORN. DISTAL CUSPS VERY VERY LITTLE WEAR ON ME). Wear is minimal with facets on the lingual side of the paracone, on the lingual side of the protocone, on the preprotocrista, and on the mmr. The occlusal outline is circular, with a mesio-buccal extension. The four main cusps are evident. The protocone is the largest, followed by the paracone and metacone of approximately the same size, whereas the hypocone is markedly reduced. A strongly developed parastyle / mesiostyle is evident, clearly separated from the paracone by a deep groove, with its own free cusp tip. (CHK DESCRIPTION OF STS 2 – SIMILAR AGE –IS IT NOT ACTUALLY A PARASTYLE – RATHER A TRUE CUSPULE). The mmr is worn and thick. The fovea anterior is a thin and deep fissure, bounded by an accessory/distal trigon crest. The latter is partly incised by the longitudinal fissure. The presence of the an accessory/distal trigon crest creates what is sometimes referred to as a double fovea anterior. The central fossa is broad and deep. There is no crista obliqua and the longitudinal fissure is continuous. The fovea posterior is at a different level from the trigon. . It is a thin and shallow fissure. It is bounded by a thick and low DMR. No additional cuspules are evident. On the buccal face, the mesiobuccal groove is long and deep, delimiting the parastyle. At its end, a tuberculum molare is present. The distobuccal groove is long and shallow. On the lingual face, the lingual groove is long, shallow and is ends gradually. A slight protuberance on the mesiolingual corner hints at the presence of a Carabelli trait. A band of hypoplastic pits is present. Similar pits are also evident on the mesial and the distal faces.

DNH 84: Left maxilla with dm1, dm2 (part) and the associated but isolated Rdm1, LM1, R and LI1. In the maxilla the developing crowns of LP4 and of LI2 can be seen.

dm1. The left tooth is in the maxilla and overall is well-preserved. The right tooth is isolated. The crown was broken in three pieces that have been glued back together. The

roots are largely intact, except for a small fragment missing from the distal face of the mesiobuccal root and from the root tip. The description of the crown refers to the left tooth, of the roots to the right tooth. Wear is minimal, and the cusps are rounded with tiny pits of dentine exposed on the protocone and the paracone. The mesial ICF is large, oval and reaches the occlusal margin. The distal ICF (as seen on the right tooth) is also large and oval. The occlusal outline is almost square, with a marked mesiobuccal extension. The four main cusps are evident. The protocone is the largest, followed by the paracone and metacone of approximately similar size and then the hypocone. There is a parastyle that merges with a thick MMR. The fovea anterior is reduced to a fissure. It is bounded distally by an enamel ridge emanating from the tip of the paracone. The central fossa is small and deep. The crista obliqua is present as a thick ridge of enamel, incised in its central part. The fovea posterior is reduced to a pit that is situated at a different level from the trigon. It is bounded by a worn and thick DMR. No additional cuspules are present. A ridge of enamel connecting the metacone to the hypocone is evident. On the buccal face, the short mesiobuccal groove delineates the parastyle. A small tuberculum molare is evident. The distobuccal groove is faint, ending gradually. On the lingual face, the lingual groove is deep and terminates with no issue. No obvious Carabelli trait is evident. On the lingual face there are tiny hypoplastic pits visible. The MB root is long and it shows two radicular canals. The DB root is short, straight and is oval in cross section. The lingual root is long and conical in shape. It is widely divergent from the buccal roots. Root tip curves buccally. Root lengths are as follows: MB 7.5 (as preserved), DB 6.4, L 8.5.

Ldm2. The tooth is in the maxilla. The crown is broken through the cusp tips of metacone and hypocone, and the distal part of the tooth is missing. The rest of the crown is well preserved. Wear is minimal, with facets evident on the paracone and on the MMR. The protocone and paracone are well developed. The MMR is thick and the anterior fovea is reduced to a fissure. The central fossa is large and deep. The crista obliqua is thick, and it is incised in its central part. On the buccal face, the buccal groove is faint. From its end, a thin edge of enamel moves on to the paracone. On the lingual face, the lingual groove is deep and terminates with no issue. A Carabelli trait is evident in the form of a deep

furrow. Tiny hypoplastic pits are evident. On the maxillary fragment part of the broken lingual root tip are exposed.

LM1. This is an unworn crown of a developing tooth. Preservation is excellent. A few millimeters of root development are evident. The occlusal outline is rhomboidal, with some disto-lingual extension. The main cusps are well-developed. The protocone is the largest cusp, while the paracone, metacone and hypocone are of approximately equal size. The MMR is thin, and it is incised in its central part. It is continuous with an enamel ridge from the tip of the paracone. An additional cuspule is evident on the MMR, flowing into the anterior fovea that is mostly obliterated. The central fossa is deep and broad. The thick crista obliqua is cut by the longitudinal fissure. The fovea posterior is thin and deep, delimited by a thick DMR, incised in its midpart. Its most mesial end is cut by a furrow that separates it from the metacone. On the buccal face, the buccal groove is very faint, ending in a tiny pit. From it a thin ridge moves onto the paracone. On the lingual face the lingual groove is very deep and long. On the mesiolingual corner, a Carabelli's trait is present in the form of a deep furrow.

R and LI1. The two developing central incisors are well preserved, except for a flake of enamel missing near the base of the right tooth. Crown formation appears not far from complete. Description refers to the right tooth. The labial face is slightly convex both MD and IC. Both corners are rounded, the distal more so than the mesial. The incisal edge has three mamelons of different sizes. Perikymata are visible, but not marked. The lingual face is concave IC and, less so, MD. The mesial corner appears more angulated, whereas the distal is more rounded. Both a MMR and a DMR are present. The DMR is more expressed.

DNH 85 Molar fragment
This is a fragment preserving only the distal part of the crown and part of the roots of a maxillary deciduous molar, probably a Ldm2. The base of the two roots is not preserved. The distal part of the metacone is present, which is slightly worn. The hypocone is well developed and it has a wear facet on its cusp tip. The posterior fovea is deep. The DMR is

low and thick. It bears an incipient cuspule in its central part. On the distal face, an oval ICF is present, although not very marked. Tiny hypoplastic pits are also present. Only 6.2 mm of the distobuccal root are preserved. The root is MD compressed with a marked groove on its mesial face. The preserved part of the lingual root is oval in section. Its length is 5.5.

sp indet

DNH 86   RM3

This is an isolated tooth in a mandibular fragment. Most of the distolingual corner of the crown is missing. Enamel flakes are also missing on the mesiobuccal and the mesiolingual corners. The distal roots are not preserved. The occlusal surface is worn to a flat table. A dentine pit is evident on the protoconid. The mesial ICF is large, concave and occupies most of the face. The occlusal outline is oval, tapering distally. No morphological details can be described, except for a deep mesiobuccal groove. The mesial roots are long, thick and tilted distally. They are fused, although the two root canals are evident. The ML part is 17.4.

The RI1 originally associated w DNH 86 is now DNH 98.

Overall morphology indicate rob.

DNH 87   Ldc

This is an isolated and overall well preserved deciduous tooth. The root is slightly abraded on its lingual side. Wear has reduced the height of the cusp, and has exposed a pit of dentine. A wear facet is present on the mesial edge of the crown. There is no mesial ICF. The distal ICF is large and subtriangular in shape. The labial crown outline is almost symmetrical. The cervical enamel line is slightly asymmetrical, with the apex of the concavity displaced mesially in respect to the cusp tip. The labial MMR and DMR are weakly developed. On the lingual face, the cervical eminence is weakly developed and skewed mesially. The MMR is thick and rounded, with a cleft distal to it. A median lingual ridge is evident, and it is placed mesially to the midline. The DMR is thinner than the mesial but evident. The root is long and conical in shape, and its apex appears still

open. It shows some degree of resorption on its labial face. Root length is: 9.8. This tooth most probably belong w DNH 44. Similar degree of wear, similar overall appearance. The overall morphology differs from other upper dc of fossil homs, namely Taung, Stw 151 and ER1590. All these have MD convex buccal face, which is lacking in DNH 87. The crown is more elongated MD and narrow BL. The specimen is attributed to rob ?

DNH 88   Ldi1

This is an isolated and well preserved deciduous tooth. The crown is heavily worn, with a large rectangular area of dentine exposed on the incisal edge. Wear has markedly reduced crown height. The wear plane is tilted slightly labially. A large distal ICF is present. The mesial ICF is not preserved. The preserved portion of the labial face is straight. On the lingual face the crown outline is triangular and is asymmetrical, displaced distally in respect to the midline. A faint cervical eminence is present. The root is long and relatively thick, and it is oval in section, with some degree of MD compression. The root tip is tilted slightly mesially and lingually. Root length is 11.7.

The other di1 of SA homs (Taung, Sts 24, SK 61) are all damaged to a different extent. Comparison is thus limited to dimensions. DNH 88 has MD and BL diameters similar to SK 61, whereas MD is smaller than Sts 24 (BL is not measurable in this specimen). On the basis of this and also for the fact that the wear plane is almost horizontal (indicative on an edge-to-edge contact, typical of P.rob) the specimen is attributed to rob ?.

DNH 89   Rdm1

This is an isolated, almost intact deciduous tooth. The enamel is missing from half of the mesial face, the mesiobuccal corner, most of the distal face and half of the lingual face. The roots are well preserved. Wear is marked, with pits of dentine of different size exposed on all the cusps. The preserved occlusal outline is almost triangular. The four main cusps are evident. The relative size of the cusps cannot be accurately assessed. The fovea anterior is reduced to a fissure. Although the enamel is missing the edj morphology suggests the presence of a parastyle, as in other deciduous dm1. The central fossa is large. The crista oblique, although worn, is present as a thick and low ridge of enamel.The fovea posterior is a long, transverse fissure that is situated at a different level from the

trigon. On the buccal face, the distobuccal groove is faint, ending gradually. On the lingual face, there is no evidence of a Carabelli trait. The roots are closed. The buccal roots are relatively thick and MD compressed. A deep groove on the mesial face of the MB and the DB roots suggests the presence of a double radicular canal. The lingual root is subconical in shape and subtriangular in section. It is widely divergent from the buccal roots. Preserved root length is: MB: 7.1, DB 7.6; Lingual 9.7.

Damage to the crown prevent assessment of morphological features discriminating between rob and non rob SA homs, such as development of tuberculum molare and of the mesiobuccal groove (Grine, 1984). At the same time others, such as the lingual aspect of the protocone inflated and vertically oriented; the low distal marginal ridge indicate affinities with other P.rob specimens from Drimolen and Swartkrans. The specimen is thus attributed to rob ?

DNH 90 LC

This is an isolated and overall well preserved crown and root. The cusp tip is broken, exposing dentine fragments inside. A small, oval mesial ICF is evident. There is no distal ICF. The preserved labial crown outline is symmetrical. The cervical enamel line is slightly asymmetrical, with the concavity distally placed in respect to the midline. The labial MMR and DMR are faint. An hypoplastic band is evident in the upper third of the crown. Lingually, the cervical eminence is strongly developed and skewed mesially. It bears and incipient cuspule The MMR is thick, with a shallow cleft distal to it. The DMR is also thick, with a deep cleft mesial to it. The median ridge, with a sharp edge, is evident mesial to the midline. The root is long and thick. It is oval in section with a MD compression. On its labial face, near the root tip periradicular bands are clearly visible. The root is still open suggesting that the tooth was still developing. Root length is 17.2. (Remove ? obvious affinities) 23.7.2015 MD and BL dimensions and morphological features of the lingual face (development of the MMR, DMR, cingulum) indicate rob.

DNH 91 LC

This is an isolated and overall well preserved tooth. The crown was broken in three pieces that have been glued back together. A tiny chip of enamel is missing on the cusp

tip. A large but not marked mesial ICF is present. The distal ICF is an irregular oval, on the disto lingual edge. The labial outline is oval, with some mesioincisal extension. The labial face is tall, markedly convex both IC and MD. On the lingual face, the cervical eminence is weakly developed and placed slightly distal to the midline. The MMR is weakly expressed, whereas the DMR is more marked. The root is long and thick. It is subtriangular in section and MD compressed, with longitudinal grooves on the mesial and distal faces. Numerous periradicular bands are clearly visible. Root apex is still open. Root length is 17.6.

Compared with canines and incisors at TM. Compares well w SK 852 lower left canine. Also meas compare well.

DNH 92   LP3

This is an isolated specimen. Preservation is good, except for an area abraded near the cervical margin of the buccal face that affects the crown and the root. The root tip is broken. Attrition is minimal with a wear facet on the mesial edge of the buccal cusp. Two adjacent ICF of different size are evident on the buccal face: one smaller, facing mesially, the other larger, facing buccally. This condition suggests that the premolar was not correctly aligned in the tooth row. The occlusal outline is almost circular, with some buccal extension. The two main cusps are not clearly delineated. There is no anterior fovea. The central fovea is deep and broad. The talonid is large. and it bears three incipient cuspulids. Morphological details of the buccal face are obscured by wear. There is a single root, relatively long and very thick. It is subtriangular in section and MD compressed, with longitudinal grooves on the mesial and distal faces. These suggest the presence of a double radicular canal. The preserved portion of the root is 16.4.

The overall appearance suggests some kind of developmental alteration that affected crown morphology. MD and BL dimensions fall below the minimum for P.rob and at the lower end of the SA Homo range. It cannot be determined whether, and to what extent, the developmental alteration also affected crown size. Taxonomic allocation is indet.

DNH 93   LI1

This is an intact and isolated tooth. On the crown a large flake of enamel is missing from the incisal half of the lingual face. The incisal edge is not preserved. The root is well preserved. Remnants of the mesial ICF are visible. The distal ICF is elongated, and it is lingually displaced in respect to the midline. The labial outline is almost trapezoidal. The preserved portion of the labial face is slightly convex both MD and IC. The enamel line is almost straight. Perikimata are evident. On the lingual face, the cervical eminence is weakly developed. A groove is present, distal to it. A large hypoplastic area is present in the central part of the face. Damage to the crown precludes description of additional morphological details. The root is long and thick. It is subtriangular in section and MD compressed. Root length is 19.5.

In terms of morphology and metrics the specimen compares well with other rob I1. The specimen is attributed to rob.

DNH 94   Ldi1

This is an isolated and very well preserved deciduous tooth. The crown is heavily worn, which has markedly reduced the crown height. A large and concave area of dentine is exposed. The lingual edge of the dentine exposure shows, in its central part, a marked concavity. The mesial ICF is large and circular. It occupies most of the mesial face and it encroaches the incisal margin. The distal ICF is large and concave. The labial face is convex MD and almost straight IC. The enamel line is almost straight. Hypoplastic pits are present in the central part of the face. On the lingual face, the cervical eminence is marked and centrally placed. A median eminence must have been present, as indicated by its sectioned profile at the incisal margin. The root is thick, conical in shape and BL compressed. Its apex is tilted lingually. There is a longitudinal groove on the labial face. Root length is 10.6.

In terms of morphology and metrics the specimen compares well with SK 839/852, SKX 16060 and SWT1/LB-15, pointing towards an allocation of the specimen to rob.

DNH 95   Rdi2

This is an isolated deciduous tooth. The crown is intact and unworn. Only a few mm's of the root are preserved on the lingual side. The labial face is subtriangular in outline, with

a mesioincisal extension. It is convex both MD and IC. The incisal edge slopes distally. The lingual face shows a weak cervical eminence and poorly developed MMR and DMR. The overall appearance of the tooth suggests that it is developmentally reduced, as sometimes the case in lateral incisors.

Hominin ?

DNH 96   L and Rdm1

This specimen comprises two isolated antimere deciduous teeth. The left tooth is very well-preserved, except for a tiny chip of enamel missing on the mesiolingual corner, near the cervical margin, and a minor crack crossing the lingual cusps. The right tooth has enamel missing from most of the mesial and distal faces, and also on the mesiolingual part on the occlusal surface of the protocone. In both teeth the roots are well-preserved. The description of the crown refers to the left tooth. The crown is worn, with small areas of dentine exposed on the mesial cusps and on the hypocone. The cusp tip of the metacone is rounded, but there is no dentine exposure. The mesial ICF is circular in shape, buccally placed in respect to the midline. The distal ICF is large, oval and reaches the occlusal margin. It is slightly lingually placed to the midline. The occlusal outline is almost square, with a marked mesiobuccal extension. The four main cusps are evident. The protocone is the largest, followed by the paracone and metacone of approximately similar size and then the hypocone. There is a parastyle that merges with a thick MMR. The fovea anterior is reduced to a fissure. It is bounded distally by an enamel ridge emanating from the tip of the paracone. The central fossa is small and deep, partly occupied by an enamel ridge connecting the paracone and the metacone. The crista obliqua is present as a thick ridge of enamel. The fovea posterior is reduced to a shallow fissure by an enamel ridge emanating from the hypocone. It is bounded by a worn and thick DMR. No additional cuspules are present. On the buccal face, a faint mesiobuccal groove delineates the parastyle. No tuberculum molare is evident. The distobuccal groove is faint, ending gradually. On the lingual face, the lingual groove is deep and terminates with no issue. No obvious Carabelli trait is evident. The MB root is long and it shows two radicular canals. Root tip curves lingually. The DB root is short, straight and is oval in cross section. The lingual root is long and conical in shape. It is widely divergent from

the buccal roots. The DB and the lingual roots shows resorption on their surfaces. Root lengths are as follows: MB 8.9, DB 10.1, L 6.9.

In terms of morphology and metrics the specimen compares well with other rob dm1. The specimens are attributed to rob.

DNH 97   RM3

This is an isolated and overall well preserved tooth. Enamel is missing from most of the lingual face and the mesiolingual corner. The tooth is heavily worn. Dentine exposure on the protoconid, metaconid and the hypoconid created a single large basin. The remaining cusps are worn flat, with no dentine exposure. There is a large mesial ICF that encroaches the occlusal margin. The occlusal outline is ovorectangular, with some distolingual extension. The heavy wear precludes description of additional morphological details. On the buccal face, a large hypoplastic area is evident in its central part. The mesial roots are long, thick and tilted distally. They are fused, although the two root canals are evident. Similarly, the distal roots are fused, straight and distally oriented. Root length is: ML 19.6 MB 16.7 DL 17.4 DB 13.6.

ROB.

DNH 98 (was part of 86) RI1

This specimen is an isolated RI1. Only a distal fragment of the crown is preserved. The root has the tip broken and the labial face abraded. On the crown fragment no morphological details can be described, except for a distal contact facet. The incisal edge is also damaged. The preserved portion of the root is long and thick, and is subtriangular in section. Root length (as preserved) measured on the labial face is 13.4.

(Cf SK 65).

Similar damage on the incisal edge, similar overall preservation, suggest possible association w DNH 93.

Taxonomic attribution: indet.

What was DNH 98 was moved to DNH 27 b and c

DNH 99 RM1

This is an isolated, partial crown of a developing tooth. The mesiobuccal corner of the crown is missing, broken through the paracone. The tooth has enamel missing from near the crown base on the mesial, lingual and buccal faces. Only part of the distal face is preserved, and it shows crown completion but no root formation. Occlusal outline appears to have been square, with the four cusps well delineated. The remaining part of the anterior fovea is a short fissure, mesially placed to the paracone. The MMR is thick and well developed. It bears two cuspules on its edge. The central fovea is large and deep. The crista oblique is thick, and it is intersected by the longitudinal fissure. The posterior fovea is a deep fissure with a trilobate shape. It is bounded distally by a low and not thick DMR. On the lingual face the lingual groove is shallow, ending with no issue. There is no Carabelli trait. No details of the buccal face can be described.

The specimen shows affinities with the other early Homo specimens from DN in the MD elongation and almost vertical lingual face. Taxonomic attribution: Homo ?

[Homo ???? cf. other DNH homo and rob specs. See sk27. Seems different from skw 3114. Different from sk47]

Category 2:

DNH 100 LM2.

This is an isolated and well preserved tooth bud. Crown formation is complete with no root formation. An enamel flake is missing on the central part of the lingual face near the cervix. The occlusal outline is ovo-rectangular, slightly compressed MD. The main cusps are well-developed with the metaconid being the largest followed by the protoconid and hypoconid of similar size. The cusps form a Y pattern. A well delineated C7 is present, reaching the longitudinal fissure. The MMR is thick and low. Incipient cuspulids are present in its central part. One of these is moving into the fovea anterior which is large and deep. A continuous distal trigonid crest is evident. The central fossa is broad and deep. The distal fovea is small but deep, bounded by a thin and low DMR. . On the buccal face the mesiobuccal groove is deep and broad, ending into a deep pit. A well developed protostylid is present. The distobuccal groove is deep and short, ending into a pit. On the lingual face two shallow parallel furrows delimit the C7.

DNH 101   RM2.

This specimen is the crown of a developing tooth. Crown formation is complete with few millimeters of root formed. Most of the disto-lingual part of the tooth (the entoconid, the hypoconulid, and most of the hypoconid) is missing. The occlusal outline appears to have been rectangular. The main cusps are well-developed. The metaconid is the largest cusp. The relative size of the others is difficult to assess. The cusps form a Y pattern. On the metaconid a faint groove delineates an incipient postmetaconid. The MMR is thick and low. On its edge a series of cuspulids and tiny pits are evident. The base of the metaconid is separated at the lingual end of the MMR by a groove. The fovea anterior is reduced to a thin and deep fissure, bounded by a distal trigonid crest. The latter is incised by the longitudinal fissure. The central fossa is broad and shallow, and it is incised by numerous grooves running from the longitudinal fissure. On the buccal face, both the mesiobuccal and the distobuccal groove are thin and deep. The mesiobuccal groove ends in a pit. The preserved portion of the lingual groove is faint.

DNH 102   LI2 and LC

This specimen comprises two associated and isolated teeth, a LI2 and a LC. Preservation is very good.

The developing crown of the LI2 is only half formed. In its most cervical part it shows a 'pavement cracking' appearance, typical of immature enamel. The labial face is convex IC and MD. The crown outline is asymmetrical, with the mesio-incisal corner being angulated while the distal corner is more rounded. A faint DMR is evident. In lingual view, the incisal edge has several mamelons of different sizes. The MMR is very faint, whereas the DMR is thick but weakly expressed. It ends in a tiny cuspule on the incisal edge. The lingual face is flat both MD and IC. Part of a faint median lingual ridge is also evident.

The crown of the Lc was also still developing. It also shows immature enamel.

The labial face is markedly convex IC and MD. The crown outline is asymmetrical. The crown tip is distally placed to the midline. The mesial edge is short and angled. The distal edge is much longer than the mesial edge and very steeply inclined. The preserved portion of the MMR is faint, whereas what is present of the DMR is marked, giving rise to an incipient stylid. There is a broad furrow mesial to it. On the lingual face, the MMR is relatively faint. The tip of the stylid on the DMR is marked. The median lingual ridge is strongly developed. It runs distally from the cusp tip as a sharp crest.

DNH 103   I

This specimen is represented by half crown of a developing lower incisor, possibly I1. Preservation is good. The crown is short of completion. The labial face is tall and almost straight IC. Perikymata are clearly visible. On the lingual face a thick and low marginal ridge is evident.

DNH 104 LM3.

This isolated tooth has only the crown preserved. It is broken just below the cervix. Preservation is good, except for a large flake of enamel missing from the cervical half of the mesial part of the lingual face. Wear has reduced the occlusal surface to an almost flat plane, with no dentine exposure. The mesial ICF is very large, flat and encroaches the occlusal margin. The occlusal outline is almost rounded in appearance. The protocone is the largest cusp, followed by the paracone, hypocone and metacone. Although the crown is worn a well developed C5 is still evident. A broad central fossa is present. The crista obliqua is deeply incised. The fovea posterior is largely occupied by the C5. A subvertical furrow on the mesiolingual corner of the crown suggests the presence of a Carabelli's trait.

DNH 105   Molar fragment.

This is a fragment of the crown of a developing molar. The preserved surface shows no morphological details, since the enamel is cracked. Enamel rods are clearly visible.

DNH 106 Left maxillary fragment with I2 or C (sockets only), isolated P3, P4 in maxilla, isolated partial M1 (mostly lingual cusps preserved, worn), and isolated M2 crown. P3 just erupted, M2 slightly worn, unusual crown morphology.

DNH 107 All isolated mandibular teeth. L and R dm1, L and R dm2, RM1 in mandibular fragment, L and R P3, RP4 (or upper molar), RM2 (or M3) LC, RC (half crown), RI1, R and L I2, labial face only (size difference with I1 suggests these two are I2). There is also a molar crown and root fragment. All permanent teeth still developing, at different stages. M1 just erupted with tiny wear facets on protoconid, hypoconid, and entoconid. Roots still developing. I1 unerupted.

DNH 108. Composite specimen with maxillary dentition. R maxillary fragment with dm2, M1, M2 (developing crown), R maxillary fragment with P3, C. Isolated teeth: Rdm1 (very worn crown, intact roots). Ldm2, distal half crown missing, roots well preserved. RI1, incisal edge damaged, LC well preserved, developing root. LP3, crown and buccal root well preserved, R and L P4. RP4 crown only well preserved, LP4 most part of the buccal face missing. LM1 MB root missing; part of lingual root missing. Crown well preserved, worn.

Category 3:

DNH 121: Ldm^2

This is a fragmentary and heavily worn tooth preserving a small segment of the Disto-Buccal root and the crown, excluding the mesial enamel. A large buccal dentine exposure occupies both the paracone and metacone. This exposure flares lingually at its distal extension and nearly joins a moderate dentine exposure on the hypocone. Small dentine exposures are also present on the protocone and along the distal marginal ridge.

The remaining occlusal surface is worn nearly flat. Occlusal outline is square. Though enamel cracking obscures the majority of crown morphology, a shallow posterior fovea is

visible. The distal ICF is large and reaches the occlusal surface. The remaining root is broken at the following distance from the cervical margin: DB = 2.8mm.

MD: 11.3mm

BL: 10.5mm

DNH 122 ("Andy's Tooth"): LM_2

This tooth preserves the crown, excluding a distal-lingual portion of the enamel reaching between the entoconid and the hypoconid, and roots, excluding the extreme tips. Occlusal outline is square with a slight mesio-lingual extension. Occlusal surface is worn mostly flat. There is a small dentine exposure on the protoconulid. A small anterior fovea is visible. The distal trigonid crest is broken by a small pit in the enamel. Both the central fovea and the posterior fovea are pronounced. The mesial ICF is large, covering the majority of the mesial face and reaching the occlusal plane. Only a small portion of the distal ICF is preserved, however it appears large and would likely have covered the majority of the distal face. A small enamel pit is visible on the buccal face between the hypoconid and the hypoconulid. Another small pit is visible on the occlusal surface between the protoconid and the hypoconid and the buccal face shows multiple hypoplastic pits.

The distal roots are fused completely to their point of breakage and the mesial roots are fused for approximately ¾ of their length. These roots are broken at the following distance from the cervical margin: DB/DL = 16.1mm, ML = 18.3mm, MB = 17.5mm.

MD: 15.6mm

BL: 14.8mm

DNH 123: Dental Row

Not described; In prep at the DITSONG Museum of Natural History.

DNH 125: Ldm_1

This is an isolated and well-preserved deciduous tooth. It is at crown completion and unerupted. The protoconid, metaconid, entoconid, and hypoconid are well developed; the

hypoconulid is small. A very small C6 is evident. The occlusal outline is rectangular aside from a large, protuberant, mesioconulid. The anterior fovea is deep, shifted slightly buccally, and bordered by a thin MMR. The posterior fovea is not distinct but instead joins with a deep central fovea. The mesiobuccal groove is deep and extends down the buccal face. The Distobuccal groove is faint. A lingual groove is also evident down the lingual face. The mesial root is mesiodistally compressed. Both roots are in early stages of development and don't extend far from the cervical margin: M = 2.7mm, D = 2.9mm.

MD: 9.3mm

BL: 7.8mm

DNH 126: Molar fragment (LM^1?)

This fragment only preserves part of the crown (hypocone [most complete] and protocone and metacone [only a small bit preserved]??) and a small portion of incomplete roots. A deep central fovea is suggested.

MD: n/a

BL: n/a

DNH 128: R$_c$ (L^c?)

This is an isolated element with enamel missing from the mesial face and a fragment of the root missing on the distal side of the tip. Heavy apical wear has greatly reduced crown height and left a large dentine exposure occupying the majority of the occlusal surface. The abraded surface slopes linguo-distally. The mesial ICF is not preserved. The distal ICF is large, occupying the entire distal face and reaching the occlusal surface. Despite wear, an accessory ridge is evident mesial to the midline. The root is long and tilted distally with a groove along the distal face suggesting the possibility of a double radicular canal. Root length = 22.7mm.

MD: 7.8mm

LL: 9.0mm

DNH 129: RP$_3$ Fragment

211

The tooth is poorly preserved with only half the crown and a portion of the lingual root remaining. Wear is moderate with small dentine exposure on the metaconid (lingual cusp). Mesial and distal ICFs both occupy their remaining faces and reach the occlusal surface. The lingual root is broken at the following distance from the cervical margin: 4.8mm.

MD: 8.3mm

BL: n/a

DNH 132: Rdm^2

This tooth is heavily fragmented, missing the entire distal face and most of the central crown, as well as large portions of all three roots and enamel along the entire mesial face and half of the buccal face. This tooth is heavily worn with dentine exposures on the paracone, metacone and hypocone. The protocone and hypocone are delineated by a deeply incised groove that continues down the superior portion of the lingual face. Due to the fragmentary nature of this tooth, much cuspal morphology has been lost. The enamel is very thin and the remaining roots display some signs of resorption. The roots are broken at the following distances from the cervical margin: L = 10.8mm; MB = 15.4mm; DB = 13.0mm.

MD: 9.9mm

BL: 12.2mm

DNH 133: RP^4

This well preserved tooth is at crown completion with minor pavement cracking and no root formation. The central fovea is deep with both buccal and lingual cusps large and pronounced. Both the MMR and the DMR are distinct though not notably thick. In overall crown size, this tooth sits beyond the range seen at Drimolen and instead falls within the range of Swartkrans *P. robustus*.

MD: 10.7mm

BL: 15.7mm

Appendix 3: MNI Reasoning and Comparisons

P. robustus:

DNH 31, DNH 88, & DNH 94:

These three specimens exhibit the correct wear stages to belong to one individual. DNH 88 and DNH 94 exhibit the same wear stage and DNH 31 shows less, as would be expected of a later erupting element. DNH 94 and DNH 31 preserve distal and mesial ICFs respectively that support attribution as one individual.

DNH 44 & DNH 87:

These two specimens exhibit the same staining, wear, and state of resorption.

DNH 49 & DNH 2:

The developmental stages of these two specimens do not *preclude* them from belonging to the same individual.

DNH 56 & DNH 57:

The developmental stages of these two specimens do not *preclude* them from belonging to the same individual. DNH 57 may be slightly older however, the variation is not too great to attribute to asymmetrical wear.

DNH 84 & DNH 81:

The developmental stages of these two specimens do not *preclude* them from belonging to the same individual.

DNH 107, DNH 89, & DNH 78:

Developmental and wear stages of these specimens do not *preclude* them from belonging to the same individual. DNH 89 may be slightly younger than DNH 107 and DNH 78 may be slightly older however, the variation is not too great to attribute to asymmetrical wear.

DNH 30 & DNH 23:

The wear stages of these specimens do not *preclude* them from belonging to the same individual.

DNH 106 & DNH 26:

The developmental stages of these specimens do not *preclude* them from belonging to the same individual.

DNH 28 & DNH 59:

The wear stages of these specimens do not *preclude* them from belonging to the same individual.

DNH 1 & DNH 4:

The wear stages of the specimens support their belonging to one individual. They also preserve distal and mesial ICFs respectively that support attribution as one individual.

DNH 41 & DNH 3:

The wear stages of these two specimens do not *preclude* them from belonging to the same individual.

DNH 128 & DNH 54:

The wear stages of these two specimens do not *preclude* them from belonging to the same individual.

DNH 21 & DNH 27:

The wear stages of these two specimens do not *preclude* them from belonging to the same individual.

DNH 15, DNH 18, & DNH 19:

DNH 18 and DNH 19 contain antimerical elements and so definitively represent one individual.

DNH 25 & DNH 77a&b:

The wear stages of these two specimens do not *preclude* them from belonging to the same individual.

DNH 14 & DNH 17:

The wear stages and staining of these two specimens do not *preclude* them from belonging to the same individual.

Early *Homo*:

DNH 42 & DNH 62:

The developmental stages of these specimens do not *preclude* them from belonging to the same individual.

DNH 67, DNH 70, & DNH 71:

The developmental stages of these specimens support their belonging to the same individual. Additionally, histological studies have identified a shared irregularity in enamel striations within these three specimens.

DNH 39, DNH 45, & DNH 100:

The developmental stages of these specimens do not *preclude* them from belonging to the same individual.

Indeterminate:

DNH 61, DNH 37, & DNH 11:

The developmental stages of these specimens do not *preclude* them from belonging to the same individual. It must be noted that these specimens are fragmentary and very little morphology remains.

Appendix 4: Development and Wear Assessment

DNH 1: LM^2

Wear is absent on the distal marginal ridge (DMR). The protocone is worn below the height of the metacone and hypocone with no dentine exposed. The presence of a distal interproximal wear facet (ICF) indicates the LM^3 was in occlusion.

DNH 2: Ldm_2

This specimen displays very light wear. The distal ICF is absent indicating M_1 was not yet erupted. The mesial ICF, however is very distinct. The roots are not yet complete (Stage G).

DNH 3: *Left maxillary fragment with M^2 and M^3*

M^2

The mesial cusps are worn flat in this specimen and little crown topography is left on the full occlusal surface. The protocone slopes mesially with a small dentine exposure apically. A distinct colour change is visible along the lingual, mesial, and part of the buccal edges surrounding the protocone, suggesting these surfaces are close to exposing dentine.

M^3

This specimen shows moderate wear on the protocone, light wear on the metacone and hypocone, and very light wear on the paracone with no dentine exposed.

DNH 4: LM^1*; Only distal cusps and buccal fragment of paracone preserved*

The occlusal surface of this specimen is worn almost flat, sloping slightly mesially. A small dentine exposure is present on the hypocone.

DNH 6: *Right mandibular fragment with RM_2, RM_3, LM_2, and LM_3; Poor preservation prevents assessment*

DNH 7: *Complete maxilla and mandible with all dentition preserved; the antimere with the best preservation was chosen for assessment*

LI₁

This element is very heavily worn. A large dentine exposure occupies the entire occlusal surface leaving on a ring of lateral enamel visible. Moderate crown height has been lost.

RI₂

This element is very heavily worn. A large dentine exposure occupies the entire occlusal surface leaving on a ring of lateral enamel visible. Some crown height has been lost.

R$_C$

This element is very heavily worn. A large dentine exposure occupies the entire occlusal surface leaving on a ring of lateral enamel visible. Some crown height has been lost. It must be noted that the R$_C$ shows slightly more wear than the L$_C$.

LP₃

This element is heavily worn with small dentine exposure on both the protoconid and metaconid. It must be noted that the RP₃ lacks the dentine exposure on the metaconid.

LP₄

This element is heavily worn with small dentine exposure on both the protoconid and metaconid. The distal ICF is large and concave.

LM₁

This element is heavily worn with moderate dentine exposures on both the protoconid and the metaconid and small dentine exposures on both the hypoconid and the hypoconulid. Both mesial and distal ICFs are large.

LM₂

This element is moderately worn with the entire occlusal surface flattened. No dentine exposure is present. It must be noted that an extremely small dentine exposure may be present on the RM₂ protoconid.

LM₃

This element is moderately worn with the rounding of the metaconid and all other cusps flattened. No dentine exposure is present. The mesial ICF is significantly concave.

LI¹

This element is heavily worn with a thick strip of dentine exposed along the incisal edge. Both the mesial and distal ICFs are large and reach the occlusal plane.

LI²

This element is heavily worn with a thick strip of dentine exposed along the incisal edge. Both the mesial and distal ICFs are large.

R^C

This element is heavily worn with a large, concave dentine exposure occupying the occlusal surface. A thick ring of lateral enamel remains. The distal ICF of both antimeres is positioned lingually while the right mesial ICF is positioned labially and the left mesio-lingually.

LP³

This element is heavily worn with a large dentine exposure on the paracone and a small dentine exposure on the protocone. Both the mesial and distal ICFs are large and the former is distinctly concave.

RP⁴

This element is moderately to heavily worn with small dentine exposures on both the protocone and the metacone. Both mesial and distal ICFs are large.

LM¹

This element is heavily worn with a large dentine exposure on the protocone and moderate exposures on both the paracone and the hypocone. Both mesial and distal ICFs are large and reach the occlusal surface. It must be noted that wear is slightly more advanced in the right antimere.

LM²

This element is moderately worn with the occlusal surface worn nearly flat. Cusps delineation is still evident. No dentine exposures are present.

LM³

This element is lightly to moderately worn with the lingual cusps worn flat and rounding of the buccal cusps. No dentine exposures are present.

DNH 8: *Mandible missing only RI₁, LI₁, and LI₂; the antimere with the best preservation was chosen for assessment*

RI₂

This element is heavily worn with a strip of dentine exposed along the incisal edge. Some crown height has been lost. The mesial and distal ICFs are small. The L_C contacts this element on the labial face while the distal ICF is positioned lingually. This suggests that the visible distal ICF may have been formed through contact with the d_c or that its position in the dental arcade shifted.

L_C

This element is heavily worn with a small dentine exposure on the apex. The mesial ICF is large and this element contacts the *RI₂* disto-lingually.

LP₃

This element is lightly worn with enamel faceting visible across the entire occlusal surface. No dentine exposures are present.

LP₄

This element is very lightly worn showing rounding on all the main cusps. No dentine exposures are present.

LM₁

This element is moderately worn with small dentine exposures on both the protoconid and the hypoconid.

LM₂

This element is lightly worn with flattened buccal cusps. No dentine exposures are present.

LM₃

This element is very lightly worn with only some flattening of the buccal cusps. No dentine exposures are present.

DNH 10: *Right mandibular fragment with M₃; only the hypoconid, hypoconulid, and partial entoconid and protoconid preserved*

The protoconid and hypoconid are worn flat while the hypoconulid and entoconid show moderate. No dentine exposures are present.

DNH 11: *Lower molar fragment; buccal fragment preserved with a partial protoconid and hypoconid preserved*

The preserved occlusal surface shows moderate wear without dentine exposures.

DNH 12: *Right mandibular fragment with M_3*

The specimen is unerupted with incomplete root formation (Stage E).

DNH 14: *RM^1*

The specimen shows extreme wear with a very large, continuous dentine exposure. Occlusal enamel is completely absent from the protocone and hypocone and partially absent from the paracone and metacone. Only an enamel rim made up of lateral enamel remains on the lingual, mesial, and distal edges. Both the mesial and distal ICFs are large and well pronounced. The roots show a small degree of resorption suggesting this tooth may have been close to shedding.

DNH 15: *(a) LM^3 (b) RM^3*

Both teeth are worn flat, only the metacone showing any topography, with no dentine exposed. The mesial ICF is distinct though the superior portion has been lost due to crown height lost through attrition. This suggests the teeth have been in contact with the M^2, and so in occlusion, for a significant amount of time despite the absence of dentine exposures.

DNH 16: *RM^1*

The specimen is worm almost flat with the fovea between the paracone and metacone as the only remaining topography. A small dentine exposure is visible on the protocone. A large mesial ICF is present while a distal ICF is absent.

DNH 17: *LP^3*

This specimen shows extreme wear. No occlusal enamel remains; the occlusal surface is occupied entirely by a large dentine exposure. Nearly all crown height has been lost and lateral enamel only remains on the lingual and buccal edges.

DNH 18: *RM₃*

This specimen is worn almost flat with some topography on the buccal portion of the occlusal surface. A very small dentine exposure is visible on the metaconid.

DNH 19: *Left mandibular fragment with P₃, P₄, M₁, M₂, and M₃*

P₃

This element has been worn flat and the superior portions of both the mesial and distal ICFs have been lost to crown height loss. A small dentine exposure is visible on the protoconid.

P₄

This element is also worn flat with a large dentine exposure extending centrally from both the mesiobuccal and mesiolingual corners. Both the mesial and distal ICFs are markedly distinct.

M₁

This element is very heavily worn. All cusps are occupied by dentine exposures, the buccal side of the occlusal surface being occupied by one continuous exposure that extends centrally. The distal ICF is large and distinct.

M₂

This element is worn flat with large dentine exposures on both the protoconid and the hypoconid and a small dentine exposure on the metaconid. The distal ICF is of moderate size while the mesial ICF is large.

M₃; only the protoconid and metaconid preserve

The preserved portion of this element is worn almost flat and the mesial ICF is large.

DNH 21: *Left mandibular fragment with M₂ and M₃*

M₂

This element is worn flat with moderate dentine exposures on both the protoconid and the hypoconid and very small dentine exposures on both the metaconid and the hypoconulid.

M₃

The buccal portion of this element is worn flat while the lingual portion shows distinct morphology. No dentine exposures are present.

DNH 22: *Right maxillary fragment with P^4, M^2, and M^3*

P^4

This element shows moderate wear sloping distally with no dentine exposures. The mesial ICF is moderately pronounced.

M^2

This element shows light wear with no dentine exposures. The mesial ICF is large and the distal ICF is not present.

M^3

This element is unerupted with incomplete roots (Stage E-F).

DNH 23: *Ld^c*

The occlusal plane of this specimen is worn nearly flat with a large dentine exposure apically. Both mesial and distal ICFs are pronounced and have lost the superior-most portion due to crown height loss.

DNH 24: *Rdi^2*

This specimen is heavily worn with a thin dentine exposure along the incisal edge. The roots are not yet complete (Stage F).

DNH 25: *LI^2*

This specimen is very heavily worn with a large dentine exposure apically. Both the mesial and distal ICFs are large and pronounced.

DNH 26: *RP_4*

This specimen is unerupted with incomplete roots (Stage F).

DNH 27: *(a) LP_4 (b) RP_4 (c) RM_1*

LP_4 and RP_4

This element is worn flat, occlusal surface sloping lingually. Small dentine exposures are visible on the mesial protoconid and both mesially and distally on the metaconid. Both the mesial and distal ICFs are markedly distinct.

RM₁

This element is very heavily worn with large dentine exposures on all cusps. Distal cusps are occupied by one continuous dentine exposure and attrition has nearly removed the large distal ICF through crown height loss.

DNH 28: L^c

This specimen is moderately worn with a dentine exposure occupying the majority of the apex. Both the mesial and distal ICFs are large with the distal ICF positioned distolingually suggesting this tooth sat slightly lateral to the typical dental arcade shape.

DNH 29: RP^4

This specimen is worn flat with the occlusal plane sloping both lingually and distally. A small dentine exposure is visible on the protocone. The mesial ICF is small while the distal ICF is large and pronounced.

DNH 30: Ldm^2

This specimen is heavily worn with a large dentine exposure on the protocone, a small dentine exposure on the hypocone, and a very small dentine exposure on the paracone. Both the mesial and distal ICFs are moderate in size and the mesial ICF has lost the superior-most portion do to crown height loss.

DNH 31: Ldi^2

This specimen is heavily worn with a dentine exposure visible along the incisal edge. The mesial ICF is large and has lost the superior-most portion do to crown height loss. The distal ICF is small and is located inferiorly.

DNH 35: *Right mandibular fragment with dm₁, dm₂, M₁, and left dm₂*

dm₁

This element is lightly worn showing only some enamel faceting on the mesial portion of the protoconid. The distal ICF is large and reaches the occlusal plane while the mesial ICF is small.

dm$_2$; left element is too poorly preserved for assessment

This element is very lightly worn showing rounding of each of the cusps. The mesial ICF is located superiorly, nearly reaching the occlusal plane and the distal ICF is not present.

M$_1$

This element is unerupted. The crown has just reached completion (Stage D).

DNH 36: *Rdm^1*

This specimen shows minimal wear focused mesially. The mesial ICF is small and the distal ICF is not present.

DNH 37: *Molar fragment; only a portion of one crown preserved*

The preserved portion shows only light wear.

DNH 38: *Ldi$_1$; non-human primate*

DNH 39: *RM^1*

This specimen is very lighty worn, showing some cuspal polish. The mesial ICF is small and the distal ICF is not present. The roots are incomplete (Stage E-F).

DNH 40: *LM^3*

This specimen is very heavily worn with a large, continuous dentine exposure occupying both the protocone and paracone. The main distal cusps are worn flat while the two distal accessory cusps show some topography. The roots show very minor resorption suggesting this tooth may have been close to shedding. The mesial ICF is large and has been largely lost due to cusp height loss. A dental carie is visible mesially at the cervical margin.

DNH 41: *Left maxillary fragment with I^2, ^{C}, and P^3*

I²

This element is heavily worn with a dentine exposure along the incisal edge. The mesial ICF is large and has lost the superior-most portion do to crown height loss. The distal ICF is also large and positioned labially.

C

This element is heavily worn with a large dentine pit apically. The mesial ICF is large and reaches the occlusal plane while the extremely large distal ICF occupies the majority of the lingual face.

P³

This element is heavily worn with a small dentine exposure on the protocone and a very small dentine exposure on the paracone. Both the mesial and the distal ICF are large.

DNH 42: *Rdm²*

The specimen is very lightly worn showing only cuspal rounding and no enamel faceting. The distal ICF is large and positioned lingually.

DNH 44: *Right hemi-mandible with d_c, dm_1, dm_2, M_1, and I_2*

d_c

This element is worn flat apically with a small dentine exposure visible. Neither the mesial nor the distal ICF is present.

dm_1

This element is heavily worn with moderate dentine exposures on the protoconid and the metaconid, a small dentine exposure on the hypoconid, and a very small dentine exposure on the entoconid. The mesial ICF is small and a distal ICF is not present.

dm_2

This element is unerupted; in crypt.

M_1

This element is unerupted; in crypt.

I_2

This element is unerupted; in crypt.

DNH 45: *RI^2*

This specimen is lightly worn with some enamel faceting on the incisal edge. The rots are incomplete (Stage F). Neither the mesial nor the distal ICF is present.

DNH 46: *Right mandibular fragment with dm2, M1, M2, and M3*

dm2

This element is poorly preserved and assessment is tenuous. Dentine exposures are present on both the entoconid and C7 and possibly present on both the hypoconid and the hypoconulid.

M1

The element is very lightly worn showing rounding of the buccal cusps. The mesial ICF is small and no distal ICF is present. The roots are not yet complete (Stage G).

M2

This element is not yet erupted. The crown has reached completion while the roots are incomplete (Stage D).

M3

This element is not yet erupted. The crown is incomplete and is still in the mineralization stage (Stage B-C).

DNH 47: *Left maxillary fragment with di^1, d^c, dm^1, dm^2, and M^1, right maxillary fragment with dm^1, and I^1, and Rdi$_2$, Rdm$_1$, and Rdm$_2$*

Ldi^1

Wear along the incisal edge cannot be determined due to breakage. The mesial ICF is small and extends nearly to the occlusal surface and the distal ICF is very small.

Ld^c

Wear cannot be determined for this element due to breakage. The roots are not yet complete (Stage F).

Rdm^1; left element is too poorly preserved for assessment

This element is lightly worn with very slight enamel faceting on the main cusps. No mesial ICF is present. The roots are not yet complete (Stage F).

Ldm^2

This element is unerupted. The crown is complete while the roots are not (Stage F).

LM^1

This element is unerupted. The crown is not yet complete showing delineation of the main cusps and 'pavement cracking' (Stage B-C).

RI^1

This element is unerupted. The crown is not yet complete showing 'pavement cracking' (Stage B-C).

Rdi$_2$

This element is moderately worn with a thin dentine exposure visible along the incisal edge. The mesial ICF is large and elongate and the distal ICF is small. The roots are not yet complete (Stage G).

Rdm$_1$

This element is lightly worn showing enamel faceting on the buccal cusps. Neither the mesial nor the distal ICF is present. The roots are not yet complete (Stage F).

Rdm$_2$

This element is unerupted. The crown is complete while the roots are not (Stage E).

DNH 49: *Ld$_c$*

This specimen is moderately worn with a small dentine exposure apically. No mesial ICF is present and the distal ICF cannot be assessed due to breakage. The roots show slight resorption suggesting this tooth may have been close to shedding.

DNH 51: *Right mandibular fragment with P$_3$, P$_4$, M$_1$, M$_2$, and M$_3$*

P$_3$

This element is worn flat with the occlusal plane sloping distally and buccally. A moderate dentine exposure is visible on the protoconid and two small dentine exposures are visible on the metaconid.

P$_4$

This element is worn nearly flat with a small dentine exposure visible on the protoconid and two very small dentine exposures on the metaconid.

M$_1$

This element is worn nearly flat with a large, continuous dentine exposure occupying the buccal cusps, and small dentine exposures on the distal portion of the hypoconulid as well as the metaconid and entoconid. The mesial and distal ICFs are both large and distinct.

M₂

This element is worn flat with small dentine exposures visible on both the hypoconid and the entoconid. The mesial and distal ICFs are both large and distinct.

M₃

This element is moderately worn with the occlusal plane sloping buccally. No dentine exposures are present. The mesial ICF is large.

DNH 52: R^c

This specimen is heavily worn with dentine exposed apically. The occlusal plane seems to slope distally and lingually though breakage makes this difficult to confirm. The distal ICF is large and positioned distobuccaly.

DNH 53: L^c

This specimen is moderately worn. The cusp is rounded with a very small dentine exposure apically. The mesial ICF is small and the distal ICF occupies the majority of the lingual face.

DNH 54: LM^3

This specimen is moderately worn with the mesial and lingual cusps worn flat. No dentine exposures are present. The mesial ICF is large and distinct.

DNH 56: *(a) Ldm₂ (b) Rdm₂*

Both teeth are lightly worn showing only very slight enamel faceting on the main cusps. The mesial ICFs are small and near the occlusal surface. The roots are yet incomplete (Stage E-F).

DNH 57: *(a) Ldm2 (b) RM1*

Ldm2

This element shows extremely light wear with enamel polish visible only on the MMR. The mesial ICF is small and near the occlusal surface while no distal ICF is present. The roots are not yet complete (Stage F).

RM1

This element is unerupted. The crown is not yet complete (Stage C).

DNH 58: *LP$_3$; only protoconid preserved*

This specimen is heavily worn with a large dentine exposure visible on the protoconid. The mesial ICF is large.

DNH 59: *RP^4*

This specimen is moderately worn with no dentine exposures present. Both the mesial and distal ICFs are large and reach the occlusal plane.

DNH 60: *Cranial fragments with associated Rdm^1, LM^1, Rdm$_1$, Rdm$_2$, RM$_1$, and RM$_2$*

Rdm^1

This element is heavily worn with large, nearly conjoining dentine exposures on both the hypocone and protocone and a small dentine exposure on the metacone. The distal ICF is large and reaches the occlusal surface. The distobuccal root shows marked resorption.

LM^1

This element is lightly worn with some enamel faceting on the main cusps. The large mesial ICF is located superiorly and s distal ICF is absent. The mesiobuccal root is not yet complete (Stage F).

Rdm$_1$

This element is heavily worn with moderate dentine exposures visible on all main cusps. Both the mesial and distal ICFs are large with the distal ICF occupying the entire face and reaching the occlusal surface.

Rdm$_2$

This element is moderately worn. Lingual cusps are rounded and buccal cusps each show a small dentine exposure. Both the mesial and distal ICFs are large with the mesial ICF occupying the entire face and reaching the occlusal surface.

RM₁

This element is very lightly worn showing only slight polish on the buccal cusps. The mesial ICF is small and a distal ICF is not present. The roots are not yet complete (Stage F-G).

RM₂

This element is unerupted. The crown is complete with no root development (Stage D).

DNH 61: *Molar fragment*

The remaining portion is worn flat with a small dentine exposure visible. A large ICF is also present on the remaining face and reaches the occlusal surface.

DNH 62: *LM¹*

This specimen is unerupted. The crown is nearly complete but still shows "pavement cracking" (Stage C-D).

DNH 67: *RM₁*

This specimen is unerupted, The crown is complete with no root development (Stage D).

DNH 68: *Right mandibular fragment with ₍c₎ fragment, P₃, P₄, M₁, M₂, and M₃; ₍c₎ is too poorly preserved for assessment*

P₃

This element is heavily worn with a large dentine exposure visible on the protoconid. Both the mesial and distal ICFs are large with the mesial ICF reaching the occlusal plane and showing a distinct concavity suggesting atypically heavy interproximal pressure between this element and the ₍c₎.

P₄

This element is heavily worn with a large dentine exposure visible on the protoconid and a small dentine exposure on the metaconid. The mesial ICF is large and reaches the occlusal plane.

M₁

This element is heavily worn showing a small dentine exposure on each of the buccal cusps. Both the mesial and distal ICFs are large and reach the occlusal surface.

M₂

This element is heavily worn with small dentine exposures visible on both the hypoconid the protoconid. Both the mesial and distal ICFs are large and reach the occlusal surface.

M₃

This element is lightly to moderately worn with the occlusal surface worn flat buccally while preserving distinct morphology lingually and distally. No dentine exposures are visible.

DNH 70: *LM¹*

This specimen in unerupted. The crown is nearing completion (Stage C-D).

DNH 71: *RI¹*

This specimen is unerupted. The crown is nearing completion (Stage C-D).

DNH 72: *L^C*

This specimen shows some occlusal wear though it is impossible to assess due to breakage. The distal ICF is long superio-inferiorly and slightly concave. The mesial ICF is not preserved.

DNH 73: *L^C*

This specimen is heavily worn with a dentine exposure visible at the apex. The mesial ICF is large and irregular in shape. The distal ICF is large and positioned lingually.

DNH 74: *LM²*

This specimen shows light to moderate wear. The protocone shows rounding while the paracone is nearly worn flat. The mesial ICF is large and reaches the occlusal surface while a distal ICF is not present.

DNH 75: *RM₃*

This specimen is unerupted. The crown is complete but the stage of root development cannot be determined due to breakage.

DNH 77: *(a) RI¹ (b) L_C*

RI¹

This element shows extreme wear. A large dentine exposure occupies the occlusal surface leaving only a ring of lateral enamel visible and the majority of crown height has been lost. Mesial and distal ICFs occupy the remaining lateral faces.

L_C

This element shows extreme wear. A large dentine exposure occupies the occlusal surface leaving only an edge of lateral enamel on the labial portion. Nearly all crown height has been lost. The root shows slight resorption suggesting this tooth may have been close to shedding.

DNH 78: *RP³*

This specimen is unerupted. The crown is complete with no root development (Stage D).

DNH 79: *(a) R_C (b) L_C*

Both teeth are unerupted. Crowns are complete but roots are not (Stage F).

DNH 80: *LI₂*

This specimen is heavily worn with a large strip of dentine exposed along the incisal edge. The mesial ICF is large and reaches the occlusal surface. The Distal ICF is also large and positioned lingually.

DNH 81: *RM₁*

This specimen is unerupted. The crown is complete with no root development (Stage D).

DNH 82: R^C

This specimen is unerupted. The crown is complete with some root development (Stage E).

DNH 83: Rdm^1

This specimen was not fully erupted. There is some evidence of cuspal polish of the lingual sides of the paracone and protocone.

DNH 84: *Left maxillary fragment with dm^1, fragmentary dm^2, and associated Rdm^1, LM^1, RI^1, LI^1, LP^4, and LI^2*

dm^1

This element is moderately worn. Very small dentine exposures are visible on both the protocone and the paracone while other cusps show rounding. Both the mesial and distal ICFs are large and the former reaches the occlusal plane.

Ldm^2

This element is lightly worn showing enamel faceting only on the paracone and the MMR.

LM^1

This element is unerupted. The crown is complete with some root development (Stage E).

I^1

This element is unerupted and the crown is not yet complete (Stage C-D).

LP^4

This element is unerupted; in crypt.

LI^2

This element is unerupted; in crypt.

DNH 85: *Distal molar fragment; likely Ldm^2*

This specimen is moderately worn with a dentine exposure visible on the preserved hypocone. A small distal ICF indicates the M^1 was erupted. The preserved root shows a small degree of resorption suggesting this tooth may have been close to shedding.

DNH 86: RM_3

This specimen is moderately worn with a flat occlusal surface and a small dentine exposure visible on the protoconid. The mesial ICF is large, concave, and reaches the occlusal surface.

DNH 87: Ld^c

This specimen is moderately worn with a small dentine exposure visible apically. No mesial ICF is present while the distal ICF is large and positioned superiorly. The root shows a small degree of resorption suggesting this tooth may have been close to shedding.

DNH 88: Ldi_1

This specimen is moderately to heavily worn with a strip of dentine exposed along the incisal edge. The distal ICF reaches the occlusal surface.

DNH 89: Rdm^1

This specimen is heavily worn with small dentine pits on all main cusps.

DNH 90: L_C

The wear of this specimen cannot be assessed due to breakage apically. The mesial ICF is small and no distal ICF is present. The roots are not yet complete (Stage F).

DNH 91: R^C or RI^2

 The wear of this specimen cannot be assessed due to breakage apically. The mesial ICF is long and narrow while the distal ICF is larger and positioned lingually. The roots are not yet complete (Stage G).

DNH 92: *LP₃ or LP₄*

This specimen is very lightly worn showing only slight polish on the mesial portion of the buccal cusp. However, this may not be indicative of the length of time in occlusion. The presence of two distal ICFs and no mesial ICF suggests this tooth was misaligned in the dental arcade.

DNH 93: *LI¹*

The wear of this specimen cannot be assessed due to breakage along the incisal edge. The distal ICF is elongate and positioned lingually while only a small portion of the mesial ICF preserves.

DNH 94: *Ldi¹*

This specimen is very heavily worn with a large strip of dentine exposed along the incisal edge. Both the mesial and distal ICFs are large. The former reaches the occlusal surface while the latter is concave and is just inferior the occlusal surface.

DNH 95: *Rdi²*

This specimen is unerupted. The crown is complete and root development cannot be assessed due to breakage.

DNH 96: *(a) Rdm¹ (b) Ldm¹*

Both antimeres are moderately to heavily worn with small dentine exposures on the paracone, protocone, and hypocone. The metacone is rounded. Both the mesial and distal ICFs are large and the latter reaches the occlusal surface. The roots show a degree of resorption suggesting this tooth may have been close to shedding.

DNH 97: *RM₃*

This specimen is very heavily worn with a large, continuous dentine exposure occupying the protoconid, metaconid, and hypoconid. All other cusps are worn flat. The mesial ICF is broad and reaches the occlusal surface.

DNH 98: *RI¹*

The state of wear of this specimen cannot be assessed due to breakage though a moderate amount of crown height has been lost. The distal ICF is large and reaches the occlusal surface.

DNH 99: *RM¹*

This specimen is unerupted. The crown is complete with no root development (Stage D).

DNH 100: *LM₂*

This specimen is unerupted. The crown is complete with no root development (Stage D).

DNH 101: *RM₂*

This specimen is unerupted. The crown is complete with some root development (Stage E).

DNH 102: *(a) L$_C$ (b) RI₂*

Both elements are unerupted. Neither crown is complete and both show "pavement cracking" (Stage C).

DNH 103: *I₁*

This specimen is unerupted. The crown is not yet complete (Stage C).

DNH 104: *LM³*

This specimen is moderately worn with the mesial and lingual portions of the occlusal surface worn flat and some topography remaining distally and buccally. No dentine exposures are present. The mesial ICF is broad and reaches the occlusal surface.

DNH 105: *Molar fragment*

This specimen is unerupted. The crown is incomplete and shows "pavement cracking" (Stage B-C).

DNH 106: *Left maxillary fragment with P³, P⁴, fragmentary M¹, and M²; root development cannot be assessed due to breakage*

P^3

This element had just recently erupted. Only slight cuspal polish is visible.

P^4

This element is unerupted.

M^1

This element is very lightly worn showing slight polish mesially.

M^2

This element is very lightly worn showing slight polish on the protocone.

DNH 107: *Ldm₁, Rdm₁, Ldm₂, Rdm₂, RM₁, LP₃, RP₃, RP₄? fragment, RM₂, RI₁, RI₂, LI₂, L_C, R_C fragment; when antimeres are present, the best preserved was chosen for assessment*

dm_1

This element is heavily worn with a flattened occlusal surface and large dentine exposures on each of the main cusps.

dm_2

This element is moderately worn with rounded cuspal morphology and very small dentine exposures on each of the main cusps.

RM_1

This element is lightly worn with small enamel facets on the main cusps. The roots are not yet complete (Stage E).

P_3

This element is unerupted. The crown is complete with no root development (Stage D).

RM_2

This element is unerupted. The crown is not yet complete (Stage B-C).

I_1

This element is unerupted. The crown is complete with some root development (Stage E).

I_2

This element is unerupted. The crown is complete with possible root development (Stage D-E).

C

This element is unerupted. The crown is complete with possible root development (Stage D-E).

DNH 108: *Right maxillary fragment with dm², M¹, M², P³, ^{C}, dm¹, I¹, P⁴, and associated Ldm², LP³, LP⁴, Lm¹, and L^C: when antimeres are present, the best preserved was chosen for assessment*

dm¹

This element is very heavily worn with all but the hypocone occupied by a large, continuous dentine exposure. The roots show a moderate degree of resorption suggesting this tooth may have been close to shedding.

dm²

This element is heavily worn with a large dentine exposure visible on the metacone, and small dentine exposures on both the paracone and hypocone. The roots show a small degree of resorption suggesting this tooth may have been close to shedding.

I¹

This element is heavily worn with a large trip of dentine exposed along the incisal edge.

C

Slight polish may be present at the apex of this element. The root is not yet complete (Stage F).

P³

This element is unerupted. The crown is complete with moderate root development (Stage E-F).

P⁴

This element is unerupted. The crown is complete with some minor root development (Stage D-E).

M¹

This element is lightly worn with all major cusps beginning to flatten. No dentine exposure is present.

M^2

This element is unerupted. The inferior portion of this element is in breccia and so root development cannot be assessed.

DNH 121: *Rdm^2*

This specimen is extremely worn with a large, continuous dentine exposure occupying the buccal half of the occlusal surface, a large dentine exposure on the hypocone, and a moderate dentine exposure on the protocone. Nearly all crown height has been lost. The roots of this specimen show near complete resorption suggesting this tooth had already been shed.

DNH 122: *LM_2*

This specimen is moderately worn with a very small dentine exposure on the protoconid, worn flat mesially, and all other cusps showing rounding. Both the mesial and distal ICFs are broad and the former reached the occlusal surface.

DNH 123: *Dental row; specimen still in breccia prep*

DNH 125: *Ldm_1*

This specimen is unerupted. The crown is complete with some root development (Stage E).

DNH 126: *Molar fragment*

This specimen is unerupted. The crown is complete with some root development (Stage E).

DNH 128: *R_c?*

This specimen is heavily worn with a large dentine exposure apically. A moderate amount of crown height has been lost. The distal ICF is large and positioned lingually. The mesial ICF cannot be assessed due to breakage.

DNH 129: *RP₃? fragment*

This specimen is heavily worn with a moderate dentine exposure on the protoconid.

DNH 132: *Rdm²? fragment*

This tooth is heavily worn with dentine exposures on the paracone, metacone and hypocone. The roots show a small degree of resorption suggesting this tooth may have been close to shedding.

DNH 133: *RP⁴*

This specimen was unerupted. The crown is complete and shows minor "pavement cracking" (Stage D).

Appendix 5: Drimolen baboon MNI data adapted from Nieuwoudt 2015

Nieuwoudt (2015) presented the Drimolen baboon MNI as follows:

	NISP:MNI Ratios			
	Craniodental	Postcranial	Total	Average MNI
Infant	21:5	25:10	46:15	7.5
Juvenile	47:8	31:9	100:23*	7.7*
Sub-adult	22:6	N/A	N/A	N/A
Adult	144:26	151:53	349:91**	30.3**
Old Adult	54:12	N/A	N/A	N/A
Total	288:57	207:72	495:129	45.5

* Juvenile total includes craniodental sub-adult category.
** Adult total includes craniodental old adult category.

Age categories were determined in a similar fashion to the methodology within this thesis (dental formation, eruption, and wear stages; Nieuwoudt 2015). However, the author does not agree with the method of MNI calculation. Due to this, for the purposes of this thesis, the final MNI was adapted following the MNI methodology presented in segment 5.2.3. That is, for the purposes of presenting the most conservative MNI, it was assumed that the postcranial material belonged to an individual otherwise represented by a craniodental specimen. While this may appear fatuous, the postcranial MNI produced here through element count did not report side (for example, 'humerus' was reported as opposed to 'right/left humerus') and so cannot be taken as a true element-count MNI. This adaption resulted in an MNI of 57.